Technical Report No. 44

STAND STRUCTURE OF A MONTANE RAIN FOREST ON MAUNA LOA, HAWAII

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PREFACE

This report gives the results of a second graduate student project in vegetation ecology concerned with the structure and dynamics of our major IBP site, an 80 hectare sample stand in an insular montane tropical rain forest. The first report dealt with the mathematical detection of species groups in horizontal space (see Technical Report No. 31), while this report is concerned with the vertical layering and population structure of the forest. The analysis technique was considered to provide for a first approximation toward a dynamic interpretation of this well preserved native Hawaiian rain forest. The report is an abbreviated version of a Master of Science Thesis in Botanical Sciences carried out under the direction of D. Mueller-Dombois. The study was supported by NSF Grant No. GB 23230 of the Island Ecosystems IRP under the US/International Biological Program and a grant provided by the Bishop Estate Corporation.

ABSTRACT

It has been suggested that the native tree species *Acacia koa* var. *hawaiiensis* Rock is not adequately reproducing and may be gradually disappearing from the montane rain forest in Hawaii. A structural analysis was carried out in an *Acacia-Metrosideros-Cibotium* montane rain forest on the east slope of Mauna Loa on the island of Hawaii, to determine the status of all woody plant species and especially the status of the tall dominant tree species *Acacia koa*. Profile diagrams were also made for systematically chosen segments in the stand. The profile diagrams showed three important structural variations within the homogenous vegetation stand. Woody plant distribution by size-classes, regardless of species, showed an inverse J-shaped distribution characteristic of a stable, self-maintaining forest. Structural analysis of individual species populations showed good stability trends for most low-stature and intermediate-stature tree species, but some species were less abundant than others. *Acacia koa* was present in all size-classes. The stand contained four times as many seedlings and suckers as tall emergent trees. Thus, this species is regenerating and maintaining itself. Low numbers of koa saplings, small trees and intermediate-sized trees may reflect rapid height growth, rather than a gradual decline of this species in the forest. Larger numbers of koa seedlings may also get established in pulses when large canopy gaps are formed. Rooting activity of feral pigs destroys *Acacia koa* seedlings rooted in mineral soil. Most of the healthy koa saplings were observed on root collars of scattered wind-thrown koa trees. This type of "gap-phase replacement" can be related to the protection seedlings receive

from pig activity. Pig populations, if allowed to increase, may cause a change in the stability trends of species populations, and an overall deterioration of this native rain forest ecosystem.

Key words: Hawaii, montane rain forest, Kilauea Forest Reserve, *Acacia-Metrosideros-Cibotium* (tree ferns) forest, *Acacia koa* var. *hawaiiensis*, *Metrosideros collina* subsp. *polymorpha* koa, profile diagrams, structural analysis, stand structure, population structure.

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INTRODUCTION

The following investigation relates to a structural analysis of a tropical montane rain forest in Hawaii. The endemic tree species *Acacia koa* var. *hawaiiensis* Rock (Leguminosae) commonly called koa, forms the tall dominant in this *Acacia-Metrosideros-Cibotium* (tree fern) forest. This forest has never been cut and thus can be considered original. However, this forest has been exposed to disturbance because of the long-term presence of feral pigs. Extensive areas which were once presumably covered by this forest type have been cleared and converted to ranchland (Whitesell 1964). As a result, this forest type is now much more restricted on the island of Hawaii. It is found in only few places, on the east flank of Mauna Kea (Mueller-Dombois and Krajina 1968), here on the east flank of Mauna Loa between 1,524 to 1,829 m (5,000-6,000 ft) (Mueller-Dombois 1966), and on the southern and western slopes of Mauna Loa and Hualalai (Nelson and Wheeler 1963).

It has been suggested that koa is not adequately reproducing and may be gradually disappearing from the rain forest (Clarke 1875, Rock 1913, Nelson and Wheeler 1963, Whitesell 1964, Scowcroft 1971). This idea was based on the observation that in many rain forests, large koa trees seem to be dying with little or no replacement by smaller ones. Clarke (1875) believed that koa was disappearing wherever it occurred as a component in the Hawaiian rain forest. He believed that koa was a seral species that would be replaced by other tree species in the forest. Rock (1913) observed many dead koa trees and several dying trees in a forest in Kealakekua, north of Honaunau. He attributed the disappearance of koa in that forest to cattle and insect activity. Nelson and Wheeler

(1963) reported that koa stands are generally open, that they show poor regeneration and contain many decadent (rotting) koa trees. Whitesell (1964) reported that 49% of the saw-timber sized (over 10.9 inches diameter at breast height) koa trees from a timber survey had excessive rot. He observed that small and intermediate-sized koa trees were absent in Acacia-Metrosideros-(Cibotium) forests in many areas. Whitesell suggested that this may be the result of high seedling mortality caused by shading in the dense forest. Scowcroft (1971) believed that light is essential for koa seeds to germinate. He noted that the light reaching the forest floor in the dense original rain forest was insufficient to induce koa seeds to germinate. He, therefore, suggested that koa decline in the original rain forest may be due to poor germination. Recently, Spatz (1973) found that light is not essential for koa germination.

Disruption of koa reproduction in some areas can be attributed to grazing by cattle (Baldwin and Fagerlund 1943) and feral goats (Spatz and Mueller-Dombois 1973) but the status of koa in the original rain forest has remained a matter of conjecture.

Since literature accounts and many verbal communications from general observations have emphasized koa as disappearing from the rain forest, this study was initiated to either verify or disprove the thesis of koa decline in the original montane rain forest.

A broader objective was to obtain data for a quantitative description of the stand structure through an analysis of all tree populations of this forest. A structural analysis of this kind was considered a first step towards an understanding of the relative stability of this forest and a prerequisite for developing critical questions for further ecological investigations.

This study was sponsored by the ISLAND ECOSYSTEMS INTEGRATED RESEARCH PROGRAM of the US/IBP, in which major emphasis has been placed on studying the structural and functional roles of species groups and their interactions in selected Hawaiian ecosystems. One aspect involves the assembling of important species groups into structural models to investigate the stability relations of these ecosystems (Berger et al. 1968). This study represents a step towards this general objective.

Field work was carried out from the winter of 1970 through the summer of 1971 by Jean Maka and myself assisted by Grant Uchida. The same set of data used in this study was analyzed by Maka (1973) to define spatially recurring species groups in this montane rain forest using a mathematical approach.

THE STUDY AREA

Physiography and soils

The study site is located in the Kilauea Forest Reserve north of Hawaii Volcanoes National Park (Fig. 1). The Forest Reserve extends as a narrow strip from 3,800 ft to 6,200 ft (1,158 m to 1,890 m) elevation on the east flank of the large active volcano, Mauna Loa. The study site itself is a plot of 80 ha size near 5,400 ft (1,650 m) elevation (Fig. 1).

The geological substrate of the study area was mapped by Stearns and Macdonald (1946) as Mauna Loa lava flows belonging to the prehistoric member of the Ka'u volcanic series.[1] The Ka'u volcanic series includes lavas from the mid-Pleistocene to present-day (Macdonald and Abbott 1970). No effort has been made to date the lavas in the study site, but these are probably less than 5,000 years old (Prof. G. Macdonald, verbal communication). The geological material at the study site is primarily a'a lava with some ash overlay. A striking feature is microtopographical drops of 3 to 6 m at several places. This type of land form has also been reported from Olaa, a rain forest area southeast of the Kilauea Forest Reserve. Stearns and Macdonald (1946) suggested that such hummocky lava would develop from microtopographical variations and sluggishness during deposition as well as from damming in the dense wet forest.

There are no well-defined drainage patterns in the study site but

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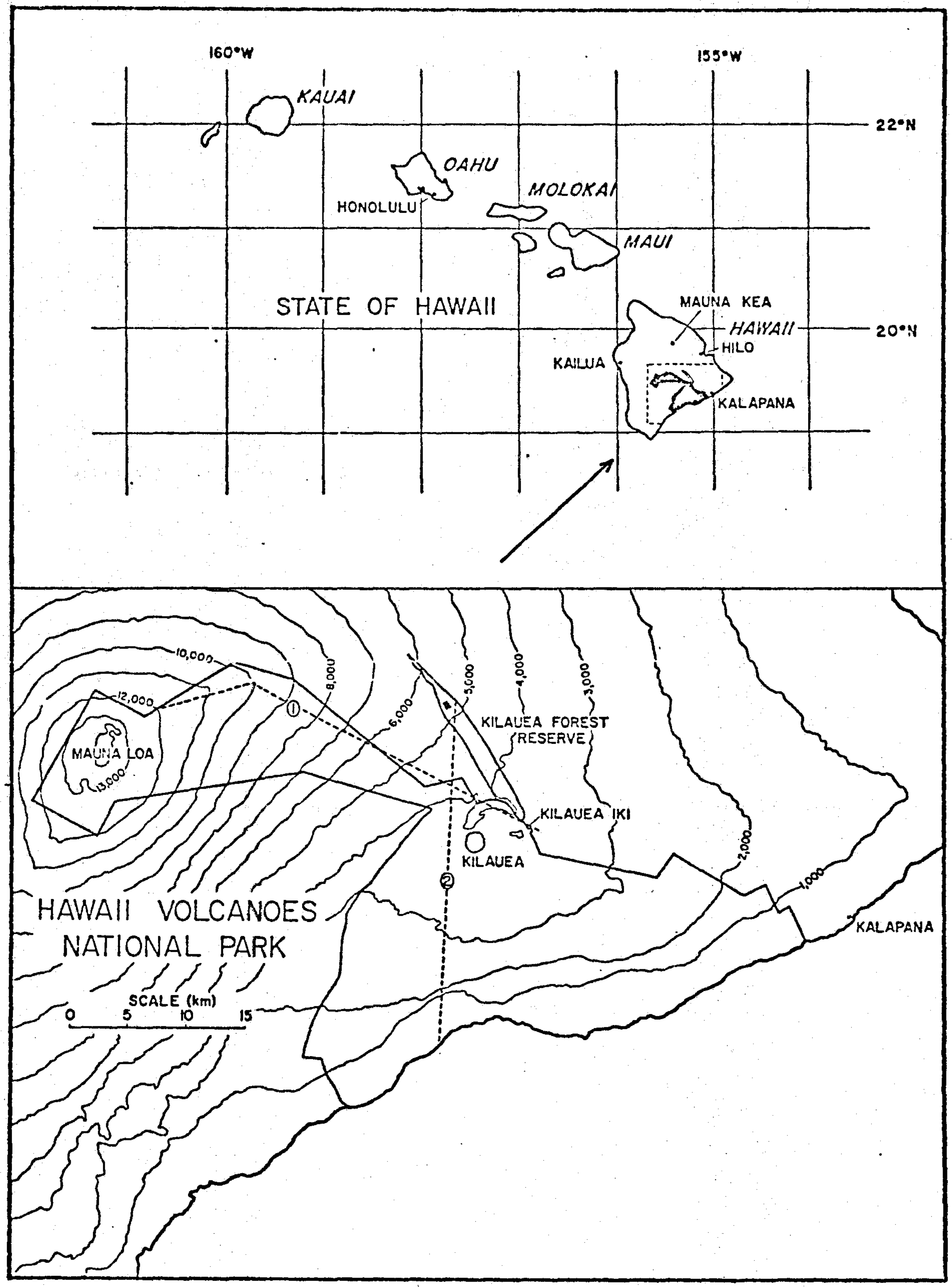
[1] In Hawaii, prehistoric lava refers to lava flows that occurred prior to 1778. Only after this date, when these islands were discovered by Capt. James Cook, were lava flows recorded.

Fig. 1. Orientation map of the Hawaiian Islands with Hawaii Volcanoes National Park and the Kilauea Forest Reserve on the southern island, Hawaii. Also shown are the locations of three IBP study sites, transect 1, 2 and the Kilauea Forest plot. The location of the latter is indicated by the black rectangle at the north end of transect 2.


160°W
155°W
22°N
20°N
KAUAI
OAHU
HONOLULU
MOLOKAI
MAUI
STATE OF HAWAII
MAUNA KEA
HAWAII
HILO
KAILUA
KALAPANA
10,000
12,000
13,000
8,000
6,000
5,000
4,000
3,000
2,000
1,000
MAUNA LOA
KILAUEA FOREST RESERVE
KILAUEA IKI
KILAUEA
1
2
HAWAII VOLCANOES NATIONAL PARK
SCALE (km)
0 5 10 15
KALAPANA

puddles and small pools are formed throughout most of the year and small creeks run downslope during rainstorms.

The soil in the study area was mapped as rockland pahoehoe lava with Pu Oo, Maile or Olinda soil material by Cline et al. (1955). In the study site, the A_1 horizon which is composed of ash with organic matter heavily admixed, lies directly on a'a lava. Because of this, the soil in the study site is better described as rockland, a'a lava with Pu Oo, Maile or Olinda soil material. Some of the Olinda soils were interpreted by Mueller-Dombois (1966a) as very shallow discontinuous ash soil on a'a. In the study site, the soil is characteristically discontinuous with semi-weathered a'a rocks exposed in many places. Because of the richness in organic material, the soil is strong brown to very dark brown in color. It has the texture of a clay loam. A well-defined litter layer is not present, but rotting logs, fallen branches and leaf litter are common on the forest floor. Recently, Sato et al. (1973) have characterized the soil in the study area as Piihonua silty clay loam on six to twenty percent slopes.

Climate

The Forest Reserve is in the cloud-fog zone and receives precipitation from both rainfall and fog drip. Based on extrapolation from Taliaferro's (1959) rainfall map, the median annual rainfall at the study area is about 1,900 mm. The mean annual temperature at the study area, computed from adjacent station records is 14°C (Mueller-Dombois 1966).

58° F

The monthly rainfall and mean monthly temperature at the IBP weather station from 1971 to 1973 plotted in climatic diagrams, using Walter's

1971 relationship of 10°C = 20 mm rainfall (Bridges and Carey 1973, 1974) showed the following. In 1971, the total rainfall was 2,516 mm, 616 mm higher than the median annual rainfall. The monthly rainfall in 1971 ranged from 587.9 mm in January to 8 mm in June. In June, the rainfall curve undercut the temperature curve in the climate diagram, indicating a short drought for that month. February and August were dry months with less than 100 mm rainfall. The total rainfall for 1972 was 1,740 mm, 160 mm lower than the median annual rainfall. No drought was recorded in any month that year, but March, May and June were dry months with less than 100 mm rainfall. The total rainfall in 1973 was 1,587.9 mm, about 312 mm less than the median annual rainfall. The monthly rainfall ranged from 456.8 mm in November to 28.9 mm in July. There were eight dry months, namely, January, February, April, June, July, August, October and December in 1973 with less than 100 mm rainfall per month. But no drought was recorded in any month of that year.

Monthly maximum, minimum and mean temperatures computed from two hourly thermograph records for the period November 1970 through December 1973, showed that monthly mean temperatures remained always between 10°C and 16°C (Bridges and Carey 1973, 1974). The mean monthly temperature for the three years 1971, 1972 and 1973 were 14.8°C, 14°C and 12.3°C respectively. In the summer, the monthly mean temperatures ranged from 13°C to 16°C. Monthly maximum temperatures from 24°C to 28°C and monthly minimum temperatures of 5°C to 10°C were recorded in the summer months. In the winter, the monthly mean temperatures were lower than in the summer and ranged from 10°C to 12°C. The monthly maximum temperatures in the winter ranged from 20°C to 24°C and the monthly minimum temperatures ranged from 2°C to 4°C. No frost has ever been recorded in the meteorological shelter (1.5 m height).

The monthly mean relative humidity for the recording period November 1970 to December 1973, showed values of greater than 90% for all months except June and August 1971, March 1972 and June, July, August and December 1973 (Bridges and Carey 1973, 1974). During these months the relative humidity was between 85% and 90%. The monthly mean maximum relative humidity reached 100% in all months of the recording period. Mean monthly minimum relative humidity reached less than 40% in February, May and October 1971, May, July and December 1972 and June, July and December 1973. The lowest minimum relative humidity was 28% in December 1972.

Vegetation and fauna

Since the Kilauea Forest and the study site lie in a year-round humid climate, it can be classified as a rain forest. Because of its altitudinal position between approximately 1,200 and 1,800 m, it is at the same time a montane rain forest (Troll 1959, Knapp 1965). Krajina (1963) described fourteen vegetation zones for the Hawaiian islands by the use of indicator species. According to his classification, the forest falls into zone 7, which contains Cheirodendron trigynum and Cibotium (tree ferns) species among others. Koa is not mentioned by Krajina as a rain forest component. This underscores the point made in the introduction that koa is not a widespread component in the Hawaiian rain forest.

Foresters (Nelson and Wheeler 1963) have classified this forest as "commercial" on account of the tall, big diameter koa trees that are scattered throughout.

The vegetation of the Forest Reserve and adjacent areas have been mapped by Mueller-Dombois (1966) at a scale of 1:12,000. The upper middle part of the Forest Reserve including the study site is mapped as an Acacia-Metrosideros forest with aborescent shrubs and Cibotium. Mueller-Dombois drew several transect profiles for map interpretation. The Kilauea koa forest appears on his transect 2 as segment 11 (Mueller-Dombois 1966:412). Transect 2 shown on Fig. 1 extends from sea level in the Hawaii Volcanoes National Park straight north to 5,000 ft (1,524 m) into the Kilauea Forest Reserve. The profile shows 11 ecosystems. It begins in a warm tropical summer-drought climate with a grassland and extends through an edaphic desert (Ka'u Desert, south of Kilauea Caldera, Fig. 1) through a mesic Kipuka forest with a summer-dry season (Kipuka Puaulu) to this humid area with the Kilauea Forest Reserve.

The montane rain forest is the habitat of a number of native bird and insect species and of several introduced mammal species. Molluscs, soil dwelling arthropods and earthworms are numerous.

Berger (1972) reported nine species of endemic birds and two introduced species from the Kilauea Forest Reserve. Tomich (1972) found Rattus rattus (house rat) abundant, Herpestes auropunctatus (mongoose) to be common and Mus musculus (house mouse), Rattus norwegicus (Norway rat) and Felis cattus (feral cat) to be rare in the forest. I saw a feral dog in September 1973, deep in the forest. It had no collar and looked emaciated. No previous records of feral dogs are known from this area although packs of feral dogs are found in other parts of the island (Tomich 1969). With its abundant food supply and cover, the montane rain forest is the favored habitat of the feral pig *Sus scrofa* (Giffin 1972). Cattle from the adjoining ranch enter the forest occasionally through broken fences, but they stay on or near the logging road. For this reason their influence on the forest so far can be considered negligible.

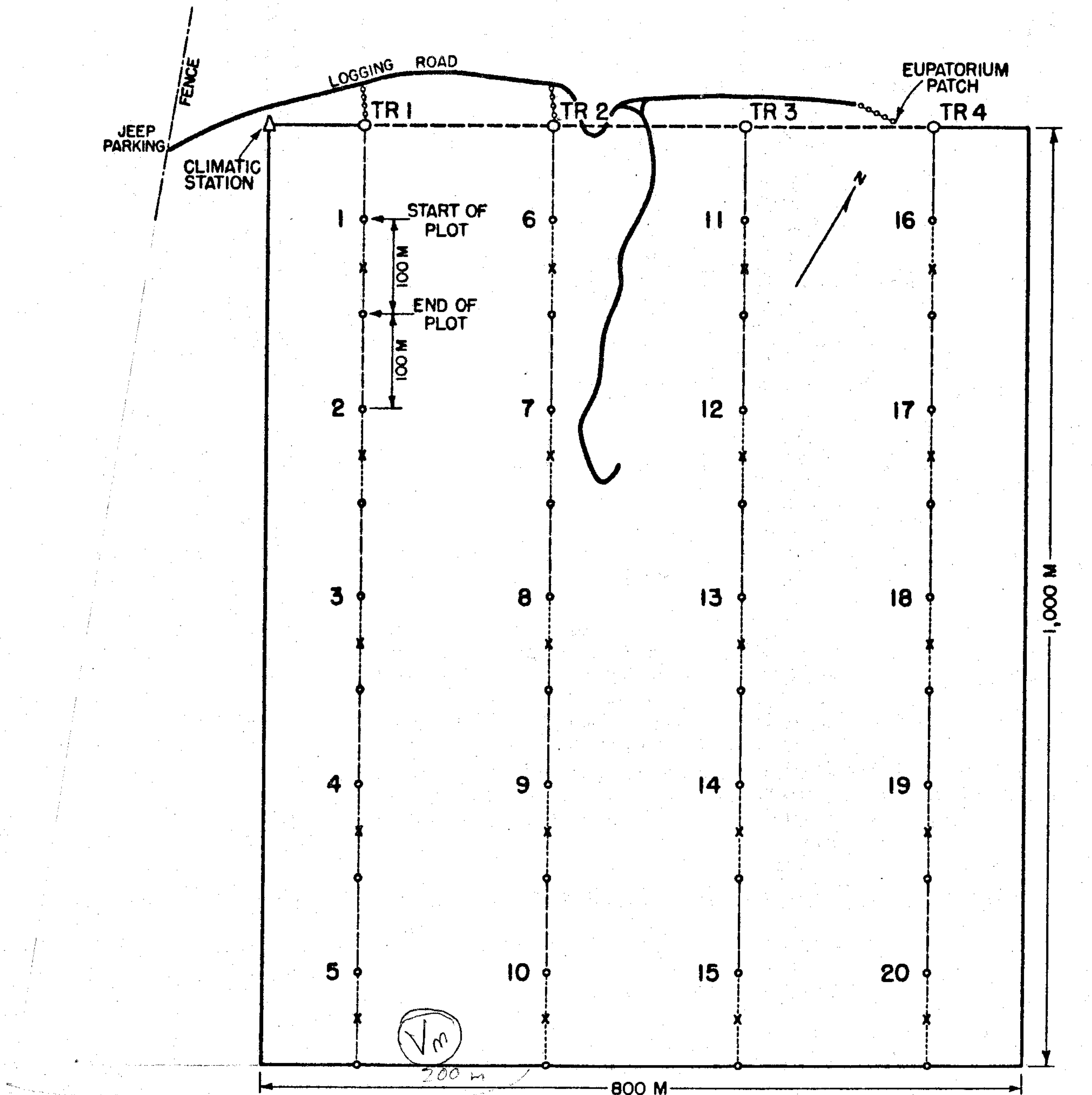
METHODS

Sampling layout

The 80 hectare (= 200 acre) study site was marked on the air-photo-based vegetation map (map sheet 8-0081 by Mueller-Dombois 1966), where it was located in the center of a homogenous tract of vegetation covering about 800 ha. The homogenity of the *Acacia-Metrosideros-Cibotium* forest study site was checked on the aerial photograph and was considered sufficient for ecological purposes. This means that information derived from the sub-samples could be pooled and averaged and then considered as representative of the forest as a whole. No further subdivision of the area was found to be necessary or advisable. The sampling layout was arranged systematically with pre-determined plot locations (Mueller-Dombois 1971, Mueller-Dombois, Cooray and Crain 1972).

An IBP climatic station formed the NW plot corner of the study site (Fig. 2). The 800 m base line was run at a 55° compass direction more or less parallel to the logging road. From this base line, four parallel transects were run, 200 m apart at 145°. On each transect, 5 plot-starting points were located. These were systematically chosen and numbered consecutively from 1 to 20. Plot-starting point 1 lies on transect 1, 100 m from the base line, plot-starting point 2 lies 200 m from point 1, plot-starting point 3, 200 m from plot-starting point 2, etc. (see Fig. 2). Plot-starting points on the other three transects were arranged in the same way.

The base line and the transect line were marked at every 5 m with colored flagging tape. The flags served as an outline for a number of



550m OUTLINE OF STUDY SITE.
BASE LINE (55° NE) WHITE FLAGS EVERY 5 METERS.
BLUE FLAGS EVERY 5 M FROM BASE LINE TO START OF PLOTS 1, 6, 11 & 16 AND BETWEEN PLOTS ON TRANSECTS. (145° SE)
ORANGE FLAGS EVERY 5 M IN PLOTS ON TRANSECTS. (145° SE)
BLUE FLAGS FROM LOGGING ROAD TO BASE LINE.
O STARTING POINTS OF TRANSECTS MARKED WITH TAG & BLUE & WHITE FLAGS.
o STARTING & END POINTS OF PLOTS MARKED WITH TAG, BLUE & ORANGE FLAGS.
x 50 M POINT IN PLOTS MARKED WITH TAG, BLUE & ORANGE FLAG.

Fig. 2. Kilauea Forest Reserve IBP study site orientation map.

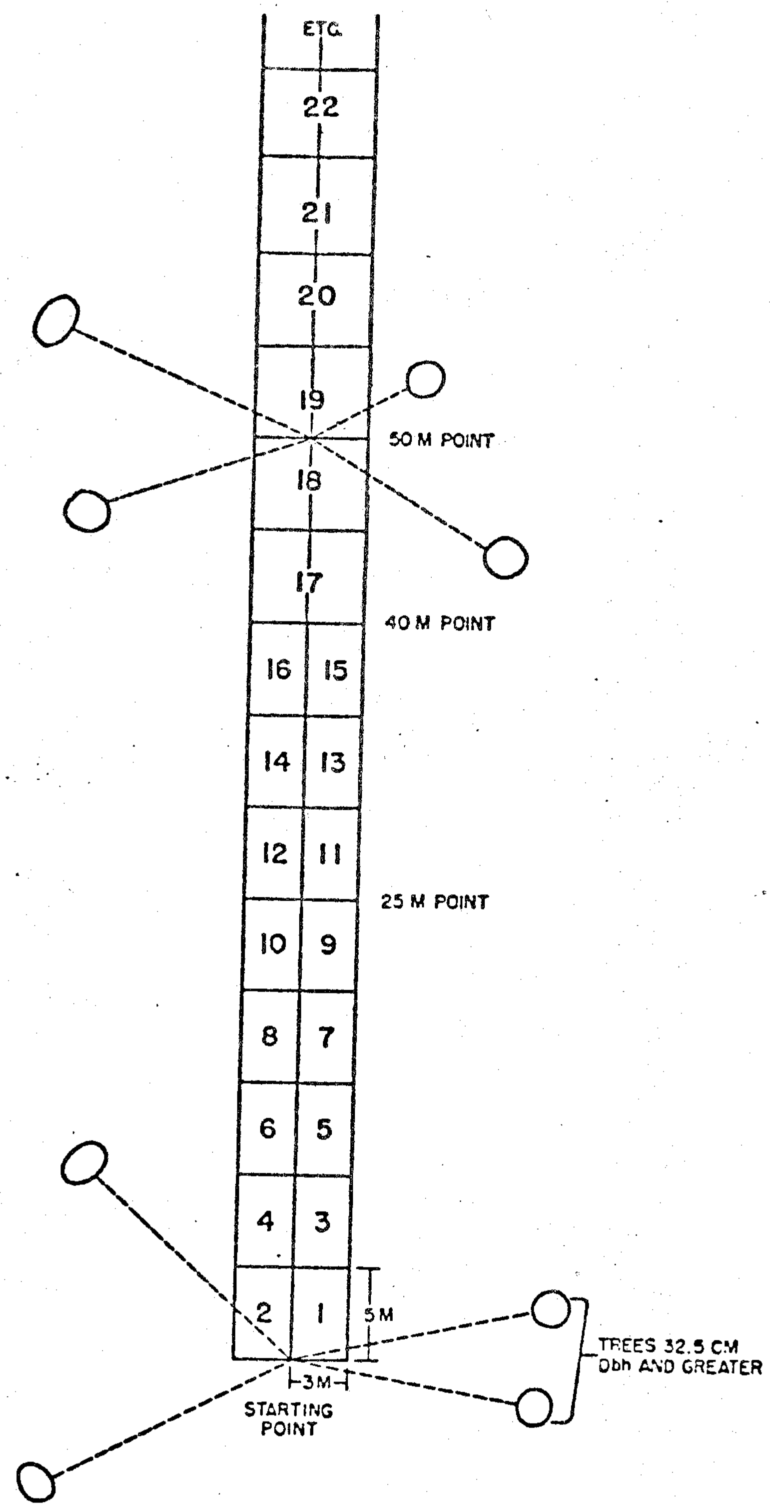
investigators working on different aspects of the same ecosystem to gain ready access to any given point on the transects for checks and resurveys when required.

From each plot-starting point, the vegetation was sampled in 5 x 3 m subplots aligned on both sides along the 145° transect line. The first subplot was laid out extending 3 m to the right (SW) of the transect and 5 m along its length. The second subplot was arranged similarly, but to the left (NE) of the center line. Further 15 m^2 subplots were added until 16 were sampled at the 40 m point (Fig. 3). From the 40 m point on up to the end of the plot at the 100 m point, the sampling area was continued in 5 x 6 m subplots which extended 3 m on each side of the center line.

Profile diagrams

Profile diagrams were made of four 6 x 50 m segments on transects 1 and 4. The segments were the first 50 m of plots 1 and 5 on transect 1 and the first 50 m of plots 16 and 20 on transect 4. The profile diagrams for woody plants over 1 m height were sketched in the field. In addition, four maps were prepared that show the ground distribution of woody plants ⩾1 m tall and tree ferns ⩾0.5 m tall which had fronds ⩾1.5 m long. Both the profile diagrams and the maps were drawn at a scale of 1:200. Data were collected on woody plant and tree fern heights, tree diameters and crown diameters in each 6 x 50 m segment. The profile diagrams for the tree ferns were drawn in the office to scale (1:200) using height measurements and field maps showing the spatial arrangements of stems of the ground. Four composite profiles were drawn by laying the woody plant profile over the tree fern profile on a light table.

Fig. 3. Map of sample plot with sixteen 5 x 3 m subplots and continuing 5 x 6 m subplots as described in text. The point-centered quarter measurements were made at the plot starting point, at the 50 m point and 100 m point. The distance to and diameter at breast height (Dbh) of any tree >32.5 cm and over 15 m tall was measured in each quarter.


ETC.
22
21
20
19
50 M POINT
18
17
40 M POINT
16
15
14
13
12
11
25 M POINT
10
9
8
7
6
5
4
3
2
1
5 M
3 M
STARTING POINT
TREES 32.5 CM Dbh AND GREATER

Vegetation sampling

Woody plant record. — Woody plants and tree ferns < 5 m stem-length were enumerated by species in reproduction and stem-length classes. Plants above 5 m stem-length were measured for diameter at breast height (Dbh) and later grouped into 5 cm Dbh classes. The ranges of reproduction, stem-length and Dbh classes are listed in Table 1. The enumeration of woody plants and tree ferns below 100 cm stem-length were made in three unequal reproduction classes. The sum of individuals enumerated in the three reproduction classes equals that of stem-length class 1. This finer breakdown of the stem-length class 1 was made to get a better idea of the reproduction characteristics of species. Stem-length was measured from the base to the apex of a plant. This criterion rather than height was important especially in the case of tree ferns because many were leaning. Moreover, tree fern fronds extended 1.5 to 2 m beyond plant apices.

Acacia koa individuals in the first two reproduction classes (i.e. below 10 cm and 10-49 cm stem-length) included both seedlings and root suckers. These two types of regeneration were separately enumerated. Each root callus ball with one or more stems arising from it was counted as a root sucker unit. Each stem arising from a root callus ball was not separately enumerated. This criterion was used in order to prevent over-estimating the number of koa root suckers. It was not possible to distinguish whether koa individuals over 50 cm stem-length have originated as seedlings or root-suckers. Thus, koa individuals over 50 cm stem-length were lumped into one group.

Sampling was first done along transects 1 and 4. All size-classes of

Table 1

The Ranges of Reproduction, Stem-length and Diameter Classes

Size class		Range in cm	
REPRODUCTION CLASSES (Plants below 1 m stem-length)			
1		below	10
2		10 -	49
3		50 -	99
STEM-LENGTH CLASSES (Plants below 5 m stem-length)			
1		below	100
2		100 -	199
3		200 -	299
4		300 -	399
5		400 -	499
DIAMETER AT BREAST HEIGHT (Dbh) CLASSES			
	class mid-point		
1	5 cm	2.5 -	7.4
2	10 cm	7.5 -	12.4
3	15 cm	12.5 -	17.4
4	20 cm	17.5 -	22.4
5	25 cm	22.5 -	27.4
6	30 cm	27.5 -	32.4
7	35 cm	32.5 -	37.4
8	40 cm	37.5 -	42.4
9	45 cm	42.5 -	47.4
etc.	etc.	etc.	

woody plants and tree ferns were enumerated in the sixteen 5 x 3 m subplots. Enumerations of individuals >50 cm stem-length were continued in twelve 5 x 6 m subplots, up to the end of each plot at the 100 m end-point. Additionally, trees (i.e. woody plants >5 m stem-length) were enumerated continuously along the two 6 x 1,000 m belt transects in 10 x 6 m subplots. In order to get a more representative sample of Acacia koa var. hawaiiensis, all size-classes of this species were also enumerated continuously along the entire lengths of these two belt transects.

After sampling transects 1 and 4 and surveying transects 2 and 3, it was felt that the essential variation in the 80 ha study site was included in the two outer transects. But for obtaining a representative sample of trees, and koa of all size-classes, enumerations of these were made also along transects 2 and 3 in continuous 6 x 10 m subplots along the entire length of these transects (i.e. 1,000 m each).

The substrate (log or soil) on which trees were established was recorded during the tree enumerations on all four transects. Any tree that showed signs of having germinated on an erect or lying tree trunk or tree fern trunk was considered log-established. These include trees germinated on logs with their root systems not reaching the ground, trees germinated on logs with their root systems reaching the ground and trees that indicated, by their present root system, that they had germinated on logs which have since decayed. All trees that did not show characteristic log-substrate establishment as described above were considered as mineral soil established.

It was clear from the reconnaissance of the forest that tall emergent (>15 m tall) trees were too scattered to be adequately enumerated in the 6 m wide belt transects. Therefore, to obtain a sufficient sample of large trees an additional sample was taken using the point-centered quarter method of Cottam and Curtis (1956).

Point-centered quarter sample. — Four emergent trees with a lower diameter limit of 32.5 cm and nearest to the sampling point in each quarter were sampled. Sampling points were at the starting point, 50 m point and 100 m point of each plot on transect 1 and 4. The four trees were each measured for their distance from the sampling point. The direction from the sampling point to each tree was also recorded. The Dbh of each tree was measured, and the substrate on which the tree was standing was noted. Dead standing trees (snags) were included in the sample but were recorded as such.

Cover sampling. — Plant height and crown-diameter data for each 6 x 50 m profile segment on transects 1 and 4 were used to map crown cover in layers. These layers were defined as, (1) trees over 15 m, (2) trees between 10-15 m and (3) trees from 5-10 m tall. Species were lumped within each layer. The crown outline of the trees was projected vertically on the 50 x 6 m belt transects with a sighting rod and mapped directly at the scale of 1:200. The cover of the tree fern layer (i.e. from 0.5-5 m height) was derived by mapping an average crown area of 12.5 m^2 (based on a 2 m average frond radius) for each tree fern individual on the tree fern stem distribution maps.

The mapped cover for each of the four forest layers was subsequently calculated with a dot-grid.

In each of the 3 x 5 m subplots, the forest floor was evaluated in percent cover seperately for exposed soil without plants, lying logs and rotting wood and outcropping rocks. The sum of the three substrate types came to be 100% for each subplot. Percent cover by bryophytes and herbaceous plants were estimated independently in these subplots.

The cover from plants ⩾0.5-5 m tall were recorded by species along the ten plots, each 100 m long in transects 1 and 4, using the line interception method (Canfield 1941).

Crown diameter (in m) and Dbh (in cm) were measured for samples of low stature (5-10 m tall) trees, by species, along the transects. The number of trees so sampled ranged from 20 trees of the less common species to 70 trees of the common species. These sample data were used to calculate regressions relating Dbh to crown diameter of the different species (Maka 1973). All trees were measured by species for Dbh. By applying the appropriate regression, the crown diameter of each low-stature individual of each species, rooted in a 6 x 100 m segment were determined. Assuming that trees have circular crowns, crown cover (in square meters) was calculated from crown diameter, using the equation for the area of a circle. The total crown cover by all individuals of each species in a 6 x 100 m segment was expressed as the percent cover for the segment.

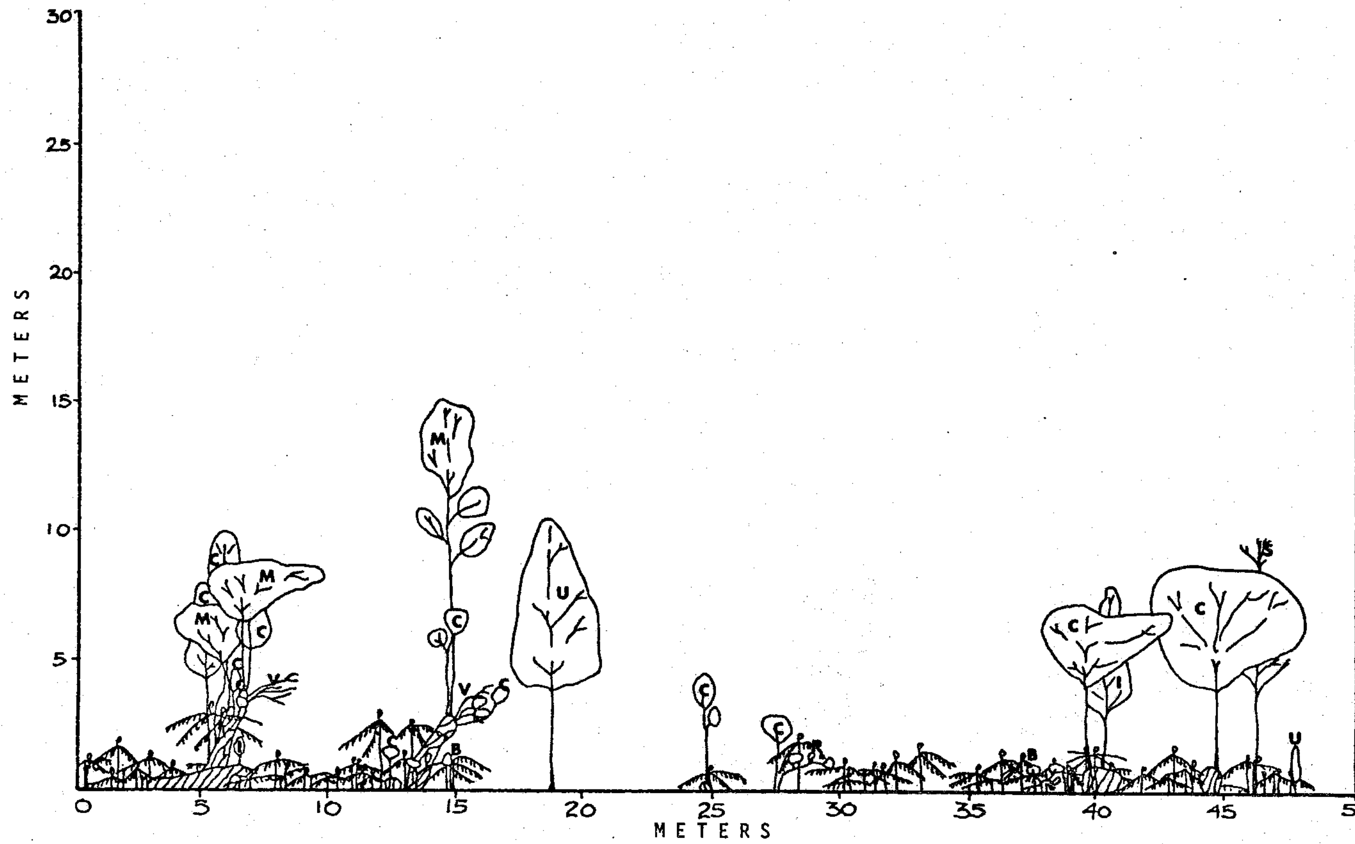
RESULTS

Layer structure of the forest

The four profile diagrams shown on Figs. 4, 5, 6 and 7 represent four systematically chosen 50 m long by 6 m wide transect-segments in the forest. Each one is different. Therefore, a single 50 m segment would not convey the characteristics of the forest. When considered together however, the four segments provide a reasonable picture of the vertical structure and plant biomass distribution in this forest. Each transect-profile may be briefly characterized as follows:

Closed tree fern patches with scattered low-stature tree groups interrupted by a gap (Fig. 4, Transect 1, Plot 1). — There are two relatively closed or continuous segments of tree ferns (*Cibotium* spp.) from 0 to 16 m and from 23 to 50 m respectively. The tree ferns occupy a stratum to about 2 m height. Groups and individuals of low-stature trees grow above the tree ferns to a height of 5-10 m. One intermediate-stature (10-15 m) *Metrosideros* individual is present at 15 m. Two tree groups can be identified, a *Metrosideros*-*Cheirodendron* group at 5-7 m and 15 m along the profile and a *Cheirodendron*-*Ilex* group at 40-45 m. It may be noted also that these tree groups are closely associated with or growing on rotting logs. In addition there are a few individually growing trees, notably *Myoporum sandwicense* at 19 m, and two smaller *Cheirodendron* individuals at 25 and 27 m, respectively. Here, it may be noted that the *Myoporum* individual grows on mineral soil in a "gap area" where tree ferns are absent over a length of 7 m, from 16-23 m.

In terms of foliar biomass, this segment shows a major, but notably interrupted occupation of the .5-2 m height stratum. Going upwards,



M - Metrosideros collina subsp. polymorpha

C - Cheirodendron trigynum

U - Myoporum sandwicense

I - Ilex anomala

R - Rubus hawaiiensis

B - Broussaisia arguta

V - Vaccinium calycinum

S - Snag

- Cibotium glaucum

- Cibotium chamissoi

- Rotting logs

Fig. 4. Composite profile diagram of 6 x 50 m strip on Transect 1, Plot 1.

there are several foliar biomass gaps in the horizontal stratum from 2-5 m, to the lower crowns of the low-stature trees. These two height strata (.5-2 m and 2-5 m) together can be characterized as the tree fern layer (.5-5 m tall). The low-stature trees occupy a height stratum from 5 m to about 10 m. This stratum is again quite open, with several larger gaps between tree groups and individuals, giving the impression of a poorly utilized "general niche" in this height-class.

Emergent tree groups with scattered low-stature trees and a closed tree fern understory (Fig. 5, Transect 1, Plot 5). — This profile segment depicts more or less the situation for which the forest has been named, namely an *Acacia-Metrosideros-Cibotium* forest. However, the emergent (up to 25 m tall) koa trees are scattered throughout the forest so that only approximately every second 50 m segment would show one or a few emergents.

The tree fern layer is denser when compared to the previous segment (Fig. 4). It is continuous. There are more tree ferns that grow taller, with their apices reaching up to 4 m height. Several low-stature tree groupings can be recognized here as on the previous segment. These are primarily *Cheirodendron* and *Ilex*, but *Coprosma*, *Pelea* and *Myrsine* join the groups indicating a greater species diversity beneath the canopy of the emergents. The latter are formed only by two species, *Acacia koa* var. *hawaiiensis* and *Metrosideros collina* subsp. *polymorpha*, that occupy a height stratum from 15-25 m with their crowns. Within this group, koa is clearly the dominant on this profile in terms of height, crown cover and diameter.

The foliar biomass layers show better space utilization on Fig. 5 than on Fig. 4 because of the addition of an emergent tree layer. The

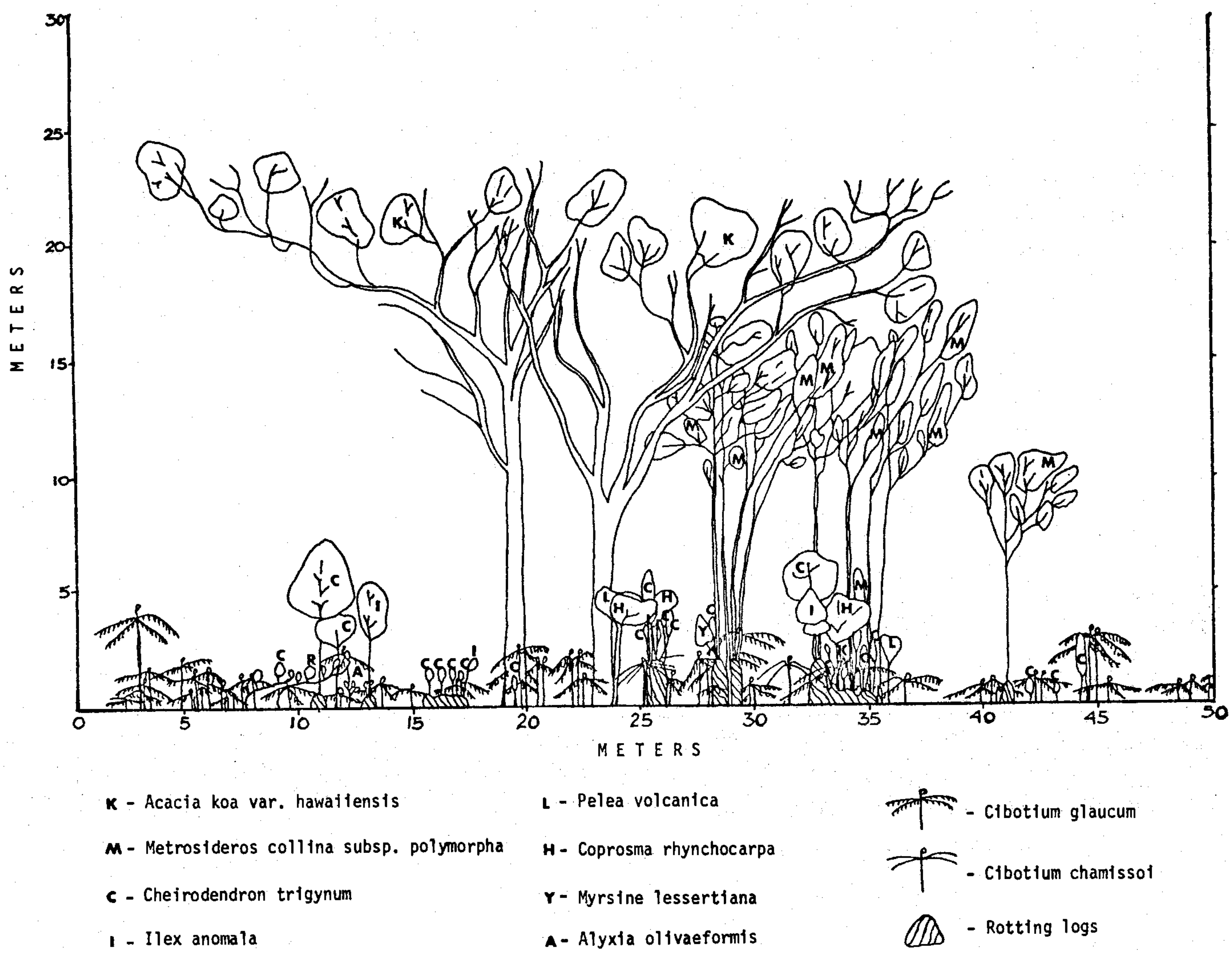


Fig. 5. Composite profile diagram of 6 x 50 m strip on Transect 1, Plot 5.

space utilization of the intermediate-stature tree layer (from about 10-15 m) and the low-stature tree layer (from about 5-10 m) appears to be generally similar to the situation shown on the previous segment (Fig. 4). In the tree fern layer (.5-5 m), the space from .5-2 m is here better utilized by the tree ferns than in Fig. 4 which showed a gap. The 2-5 m height stratum shows gaps, but it is also better utilized here than on the previous segment. This stratum also has a greater diversity of woody plant species than the previous segment (Fig. 4).

Open forest with intermediate- and low-stature trees and tree groups and a closed tree fern understory (Fig. 6, Transect 4, Plot 16). — This segment appears to be typical of the *Metrosideros*-*Cibotium* rain forest without *Acacia koa* var. *hawaiiensis* that is widespread at somewhat lower elevations on Mauna Loa and at similar elevations on the windward side of Mauna Kea. Therefore, a single 50 m long belt transect is not sufficient to portray the special characteristics of this montane rain forest. The profile in Fig. 6 is similar to that on Fig. 4. Both show only two important woody plant strata. The tree fern layer is continuous (on Fig. 6). As on Fig. 4, a *Metrosideros*-*Cheirodendron* tree group can be recognized at 8-10 m. The intermediate-stature (10-15 m) tree layer is composed solely of one species, *Metrosideros collina* subsp. *polymorpha*. This layer shows better space utilization here (Fig. 6) than in Figs. 4 and 5. The low-stature tree stratum (5-10 m) is quite similar to those on the two previous segments. In the tree fern layer (0.5-5 m), the space from 2-5 m is utilized similarly as in the previous segment (Fig. 5). It also shows a few more woody plant species (such as *Coprosma*, *Ilex*,

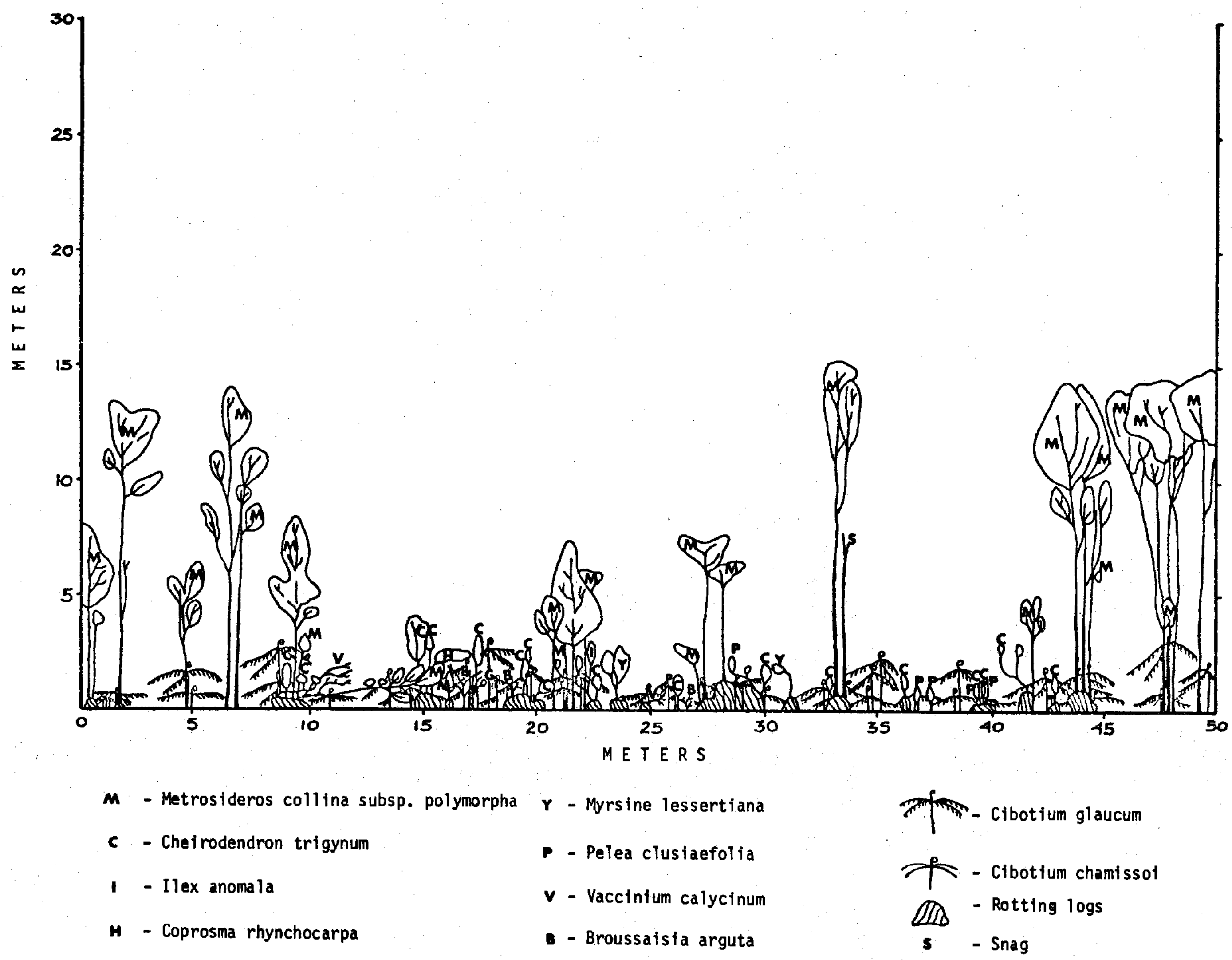


Fig. 6. Composite profile diagram of 6 x 50 m strip on Transect 4, Plot 16.

Myrsine and _Pelea_), similarly as on Fig. 5.

Because of the generally taller _Metrosideros_ individuals on this profile (Fig. 6), one could hypothesize that this segment represents an older stage in the development of this forest than is shown in Fig. 4, provided that the soil and general physical environment are the same for both.

Closed, low-stature tree group with a koa emergent and a closed tree fern understory (Fig. 7, Transect 4, Plot 20). — The emergent koa makes this transect-profile appear to be most similar to that on Fig. 5. For the same reason, it also may be said to characterize closely the situation for which the whole forest is named. However, in contrast to Fig. 5, the profile in Fig. 7 shows a relatively dense group of low-stature (up to 5 m tall) _Metrosideros_ and _Cheirodendron_ individuals. The crowns of a few _Metrosideros_ individuals reach just beyond 10 m height into the intermediate-stature tree layer. Similar, locally closed _Metrosideros_ tree groups (as shown on Fig. 7) occur at various places throughout the forest. Because of their uniform size, they can also be assumed to be even-aged. The _Metrosideros_ tree group is associated with lying logs from 4 to 34 m along the profile (see Fig. 7). It can be hypothesized that this _Metrosideros_ tree group became established on a clump of fallen logs, probably of koa after the trees broke down, and that the group represents one form of "gap-phase" replacement in the forest. From a structural viewpoint, the closed _Metrosideros_ group is just one other variation of this forest, where low-stature trees make good use of the space. The tree fern layer is dense and continuous as in Figs. 5 and 6, but in this segment it contains a larger number of species in the 2-5 m stratum. Also, the tree ferns in this segment are generally

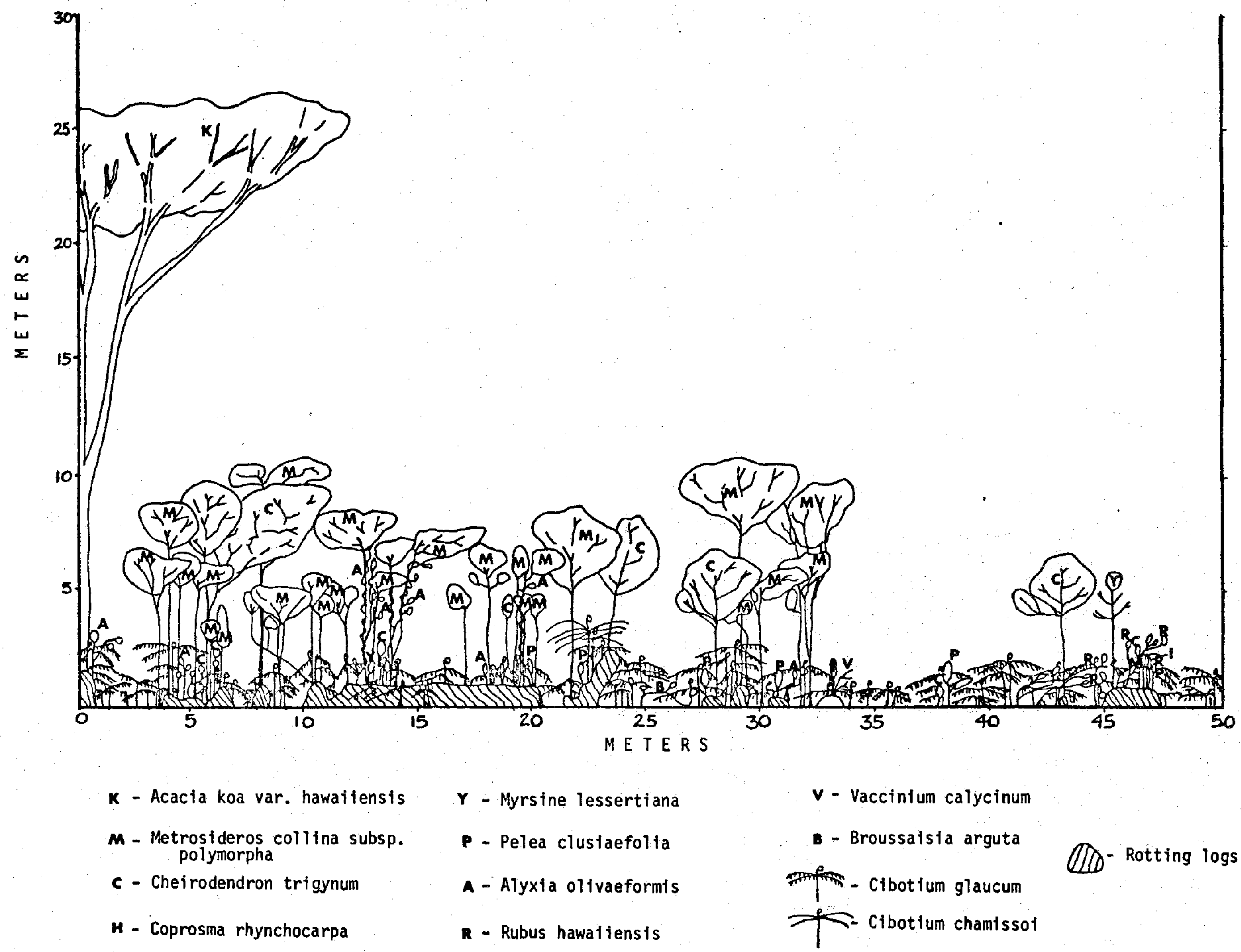


Fig. 7. Composite profile diagram of 6 x 50 m strip on Transect 4, Plot 20.

taller than on Fig. 5.

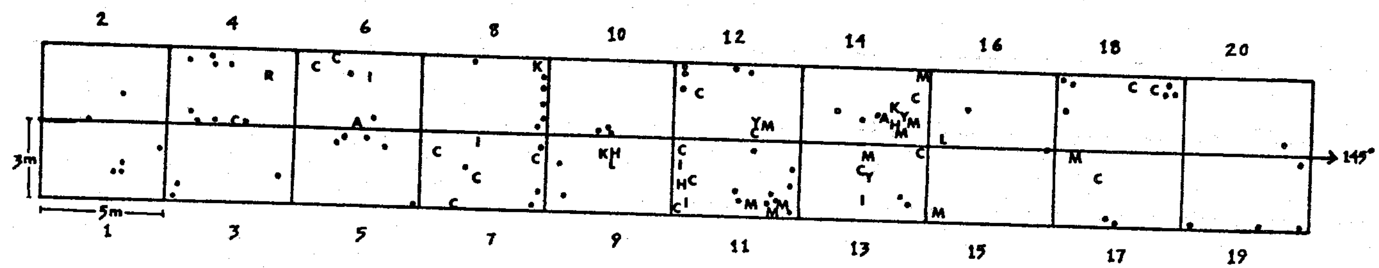
Quantitative relations between woody plant layers

The quantitative relations between woody plant layers in the forest can be evaluated for each species by two parameters, cover and density. Crown cover in the different above-ground forest layers, stem-cover or basal area and herbaceous shoot cover, all express the degree of horizontal space utilization. Since the relative saturation of space is a factor determining "niche availability," cover is an important parameter to be considered. Density provides an assessment of the structure in quantitative terms and gives information on the numerical relationships of different species in the different layers. This is useful in understanding the maintenance trends of the forest.

Cover variation among woody plant layers. — Stem distribution maps such as the one shown in Fig. 8, for the first 50 m of Transect 1, Plot 5, were made for all four profile segments (Figs. 4-7). These maps show the horizontal distribution of woody plants over 1 m tall and tree ferns over 0.5 m tall on four 50 m long by 6 m wide profile segments. Fig. 9 shows the crown cover map of the segment shown in Fig. 8. Such crown cover maps were made for all four profile segments.

The cover for each of the four layers was determined by using map-diagrams as follows:

(a) The crown outline of the trees was projected vertically on the 50 x 6 m profile-segments with a sighting rod and mapped directly at the scale of 1:200. In this process a separation was made of the three height strata, i.e. trees over 15 m, trees between 10-15 m and trees from 5-10 m tall, but species



K - Acacia koa var. hawaiiensis

M - Metrosideros collina subsp. polymorpha

C - Cheirodendron trigynum

I - Ilex anomala

L - Pelea volcanica

H - Coprosma rhynchocarpa

Y - Myrsine lessertiana

A - Alyxia olivaeformis

• - Cibotium glaucum

∘ - Cibotium chamissoi

Fig. 8. Floor diagram of 6 x 50 m strip on Transect 1, Plot 5. The profile was viewed from the side of the odd-numbered subplots.

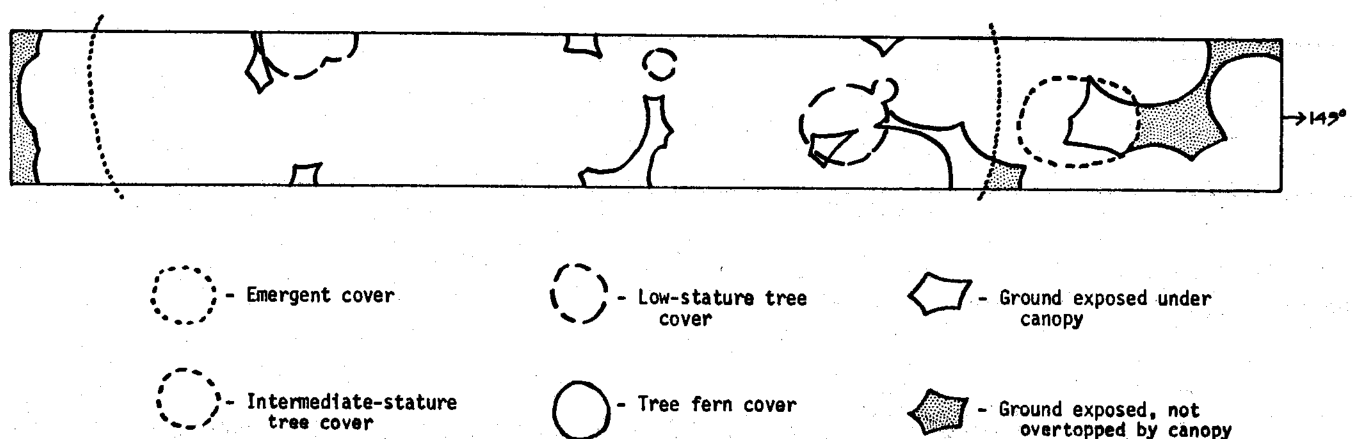


Fig. 9. Crown cover map of 6 x 50 m segment on Transect 1, Plot 5.

were lumped.

(b) The cover of the tree fern layer (i.e. from 0.5-5 m height) was derived by mapping an average crown area of 12.5 m^2 (based on a 2 m average frond radius) for each tree fern on the tree fern stem distribution maps.

(c) The mapped cover for each of the four woody plant layers was subsequently calculated with a dot-grid.

Fig. 10 shows the cover contribution by each of the four forest layers on each of the four 6 x 50 m transect-profile segments, the mean cover for the four forest layers on the four transect-profile segments and the mean cover for the whole sample (i.e. 10 plots each 6 x 100 m for the tree fern layer and 40 plots each 6 x 100 m for the low-stature tree layer). The cover of the tree fern layer is consistently high on all four transect profile segments, ranging from 75% on plot 1 to 95% on plot 5. The mean cover value for the tree fern layer for the four transect-profile segments compares well with the percentage cover value of this layer for the whole sample obtained by the line-intercept method. The value for the whole sample is the average percent line-interception of 10 plots, each 6 x 100 m.

The cover of the low-stature tree layer is less than 40% on all four transect-profile segments. The highest percentage cover (36%) for this layer is in plot 20, which showed gap-phase regeneration of Metrosideros (Fig. 7). In two of the transect-profile segments, in plot 5 and plot 16, the low-stature tree cover was below 10%. The cover of this layer for the whole sample (40 plots each 6 x 100 m) in Fig. 10 (i.e. 30.5%) was calculated by summing the crown cover of all low-stature trees regardless of species obtained from the Dbh-crown cover regression

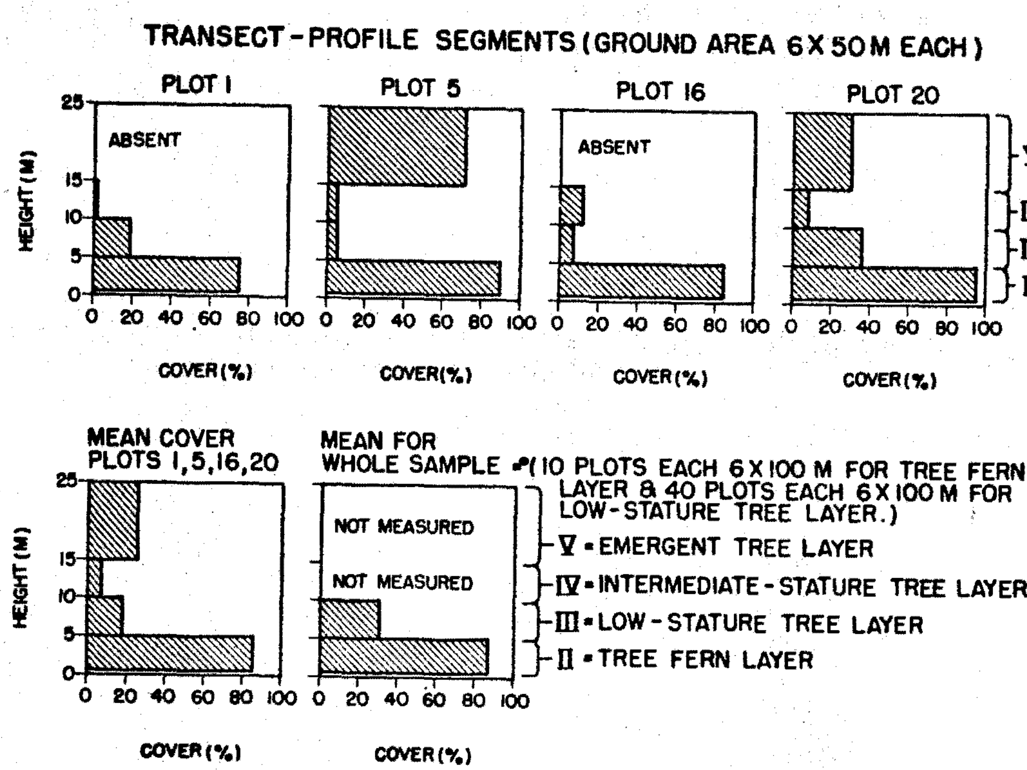


Fig. 10. Layer diagrams showing variation of cover in the Acacia-Metrosideros-Cibotium rain forest.

analysis. This was then expressed in percent of the total sample area. Since crown overlaps were disregarded, the mean cover value for the low-stature tree layer is slightly exaggerated. However, this value is closest to that of plot 20, which showed gap-phase regeneration of *Metrosideros*. This may suggest that gap-phase regeneration may be more prevalent in other parts of the forest.

The intermediate-stature tree layer had the smallest percent cover. The highest value for this layer was 12% in plot 16. In the other three plots this layer had values less than 10%. The cover for this layer which is primarily from *Metrosideros* was not measured for the whole sample.

The emergent trees were represented only in two of the transect-profile segments in plots 5 and 20. The mean percentage cover of emergent trees on the four plots was 25.5%. The percentage cover of the emergents for the whole forest was not measured, but was estimated to be about 75%. Most of the cover for this layer (65 to 70%) is from emergent *Acacia koa* (Maka 1973).

Crown and shoot cover contribution by species in the forest layers. — Table 2 lists the percent cover of individual species for the 100 m long plots corresponding to each of the four belt transect segments (plots 1, 5, 16, 20) shown as profile diagrams (Figs. 4-7) in the preceding section. Cover was calculated separately for the lower two of the three height layers and for individual species in all three layers using different techniques as follows:

(1) The cover for each of the two lower height layers of the forest was computed as follows:

(a) The percent cover of the herbaceous plant layer (cover of

Table 2

Cover Contribution (%) by Species in Three Height Layers of the Forest

LAYER Species	Individual Transect Plots 1	5	16	20	Mean Plots 1, 5, 16, 20	Whole sample
HERBACEOUS PLANT LAYER (0-50 cm tall)[a]	19.5	32.5	26.9	33.1	28.0	26.7
Carex alligata	0	0.3	1.0	0	0.3	1.7
Dryopteris paleacea	+	0.2	3.9	0.2	1.1	1.1
Carex macloviana	0.6	0.8	0.8	0.8	0.8	0.8
Veronica serpyllifolia	0	+	0.2	0	+	0.5
Adenophorus tamariscianum var. tripinnatifidum	0.4	0.4	2.4	+	0.8	0.4
Athyrium microphyllum	+	1.3	0.4	+	0.4	0.4
Cibotium glaucum	0.1	0.3	0.3	0.2	0.2	0.4
Nertera granadensis	0	0.2	0.2	0	0.1	0.3
Sadleria pallida	0	0.2	0	0	+	0.3
Athyrium sandwichianum	0.2	0	+	+	+	0.2
Metrosideros collina subsp. polymorpha	0.1	0.1	+	+	+	0.2
Broussaisia arguta	+	0	0.9	+	0.2	0.1
Cheirodendron trigynum	0.1	0.1	+	0.1	+	0.1
Rubus hawaiiensis	0.1	0.1	+	+	+	0.1
Vaccinium calycinum	0.1	0.1	0.1	0.1	0.1	0.1
Vandenboschia davallioides	+	0.9	+	0.2	0.3	0.1
Acacia koa var. hawaiiensis	+	+	+	0	+	+
Asplenium lobulatum	0.2	0.2	0	0	0.1	+
Dryopteris glabra	0.1	0.1	0.2	0.1	0.1	+
Astelia menziesiana	0	0.2	0	+	+	+
Erechtites valerianaefolia	0	0	0	0.2	+	+
Grammitis hookeri	0.1	0	0	0.1	+	+

Table 2. (Continued) Cover Contribution (%) by Species in Three Height Layers of the Forest

LAYER Species	Individual Transect Plots 1	 5	 16	 20	Mean Plots 1, 5, 16, 20	 Whole sample
Ilex anomala	0.1	0.1	+	+	+	+
Peperomia leptostachya	0	0.3	+	0	+	+
Pleopeltis thunbergiana	+	0	+	+	+	+
Polypodium pellucidum	+	0	0.2	0	+	+
Ludwigia sp.	*	*	*	*	*	3.3
Hydrocotyle sibthorpioides	*	*	*	*	*	1.9
Hypericum mutilum	*	*	*	*	*	1.3
Rubus rosaefolius	*	*	*	*	*	0.5
Veronica plebeia	*	*	*	*	*	0.4
Asplenium contiguum	*	*	*	*	*	0.2
Cibotium chamissoi	*	*	*	*	*	0.2
Coprosma rhynchocarpa	*	*	*	*	*	0.2
Dryopteris sp.	*	*	*	*	*	0.2
Holcus lanatus	*	*	*	*	*	0.2
Juncus planifolius	*	*	*	*	*	0.2
Pteridium aquilinum var. decompositum	*	*	*	*	*	0.2
Elaphoglossum hirtum	*	*	*	*	*	0.1
Pelea clusiaefolia	*	*	*	*	*	0.1
Alyxia olivaeformis	*	*	*	*	*	+
Asplenium normale	*	*	*	*	*	+
Clermontia hawaiiensis	*	*	*	*	*	+
Cyanea sp.	*	*	*	*	*	+
Cyrtandra lysiosepala	*	*	*	*	*	+
Dicranopteris emarginata	*	*	*	*	*	+
Elaphoglossum wawrae	*	*	*	*	*	+
Epilobium cinereum	*	*	*	*	*	+

Table 2. (Continued) Cover Contribution (%) by Species in Three Height Layers of the Forest

LAYER Species	Individual Transect Plots 1	 5	 16	 20	Mean Plots 1, 5, 16, 20	 Whole sample
Gnaphalium sp.	*	*	*	*	*	+
Lycopodium cernuum	*	*	*	*	*	+
Lycopodium serratum	*	*	*	*	*	+
Marattia douglasii	*	*	*	*	*	+
Myoporum sandwicense	*	*	*	*	*	+
Myrsine lessertiana	*	*	*	*	*	+
Pelea volcanica	*	*	*	*	*	+
Pipturus hawaiiensis	*	*	*	*	*	+
Sphaerocionium obtusum	*	*	*	*	*	+
Sphenomeris chusana	*	*	*	*	*	+
Stenogyne calaminthoides	*	*	*	*	*	+
Xiphopteris saffordii	*	*	*	*	*	+
TREE FERN LAYER (0.5-5 m tall)[b]	80.0	73.1	92.3	94.0	84.8	86.7
Cibotium glaucum	77.0	72.0	84.0	89.5	80.63	77.3
Cheirodendron trigynum	2.5	1.3	4.5	+	2.1	1.5
Broussaisia arguta	2.0	+	1.0	+	0.8	1.1
Rubus hawaiiensis	+	0.2	+	1.0	0.3	0.9
Coprosma rhynchocarpa	0	+	2.2	3.0	1.3	0.8
Metrosideros collina subsp. polymorpha	+	+	0.5	+	0.1	0.5
Vaccinium calycinum	+	+	+	0.2	+	0.5
Ilex anomala	+	+	+	0.1	+	0.4

Table 2. (Continued) Cover Contribution (%) by Species in Three Height Layers of the Forest

LAYER Species	Individual Transect Plots 1	 5	 16	 20	Mean Plots 1, 5, 16, 20	 Whole sample
Myrsine lessertiana	0	+	2.0	+	0.5	0.2
Pelea clusiaefolia	+	0	+	0.5	0.1	0.1
Acacia koa var. hawaiiensis	0	0	0	0	0	+
Cyrtandra lysiosepala	0	0	0	0	0	+
LOW-STATURE TREE LAYER (5-10 m tall)	37.1	22.1	25.3	60.6	36.2	30.5
Metrosideros collina subsp. polymorpha	6.2	7.9	17.0	18.9	12.5	12.9
Cheirodendron trigynum	17.1	10.0	7.7	38.2	18.3	12.0
Myoporum sandwicense	2.7	0	0	0	0.7	2.5
Ilex anomala	11.1	0.7	0	0	3.0	1.2
Myrsine lessertiana	0	0	0.6	3.2	1.0	0.9
Coprosma rhynchocarpa	0	2.3	0	0	0.6	0.8
Pelea clusiaefolia	0	0	0	0.3	0.1	0.1
Pelea volcanica	0	1.2	0	0	0.3	0.1
Acacia koa var. hawaiiensis	0	0	0	0	0	0.04

a Cover for herbaceous plant layer based on estimated percentage values from sixteen 5 x 3 m subplots in a plot (= 6 x 100 m each) expressed as percentage cover for whole plot. Mean cover for whole sample is based on average percentage cover for ten 6 x 100 m plots. Cover for individual species were recorded in sixteen 5 x 3 m subplots in a plot (= 6 x 100 m each) by Braun-Blanquet cover-abundance rating. The mid-points of the cover percentage range for

Table 2. (Continued) Cover Contribution(%) by Species in Three Height Layers of the Forest

each species was used to compute the percentage cover for whole plot.

\+ Present in plot but with < 0.1% cover.

* Absent in individual transect plot.

b Cover for the tree fern layer and cover for individual species in the layer based on % interception on a 100 m long line in each plot. Mean for whole sample based on % line interception on ten 100 m long lines.

c Cover for low-stature tree layer equals sum of % cover by individual species in a plot each 6 x 100 m. Mean for whole sample based on forty 6 x 100 m plots.

herbaceous plants and bryophytes) was estimated in sixteen 3 x 5 m subplots for each 6 x 100 m plot and expressed as a percentage value for the plot. The individual transect-plot values in Table 2 refer to the plots used for the four transect-profiles. The mean for the whole sample in Table 2 is based on the cover values for ten 6 x 100 m plots.

(b) For the tree fern layer (0.5-5 m tall) the individual transect plot cover values in Table 2 relate to a 100 m line-intercept sample for each plot. The mean for the whole sample is based on cover values for ten 6 x 100 m plots.

(2) The cover for individual species was estimated for the herbaceous plant layer and measured for the tree fern layer and the low-stature tree layer as follows:

(a) The cover of herbaceous plants (0-0.5 m tall) by species was estimated on the Braun-Blanquet cover-abundance rating scale in sixteen 3 x 5 m subplots in each 6 x 100 m plot, and converted to quantitative average values as reported in Maka (1973). The mean for the whole sample is based on the individual species cover values for ten 6 x 100 m plots.

(b) For 0.5-5 m tall individuals (the members of the tree fern layer), the species cover values shown in Table 2 relate to a 100 m line-intercept sample for each plot. The mean for the whole sample is based on the individual species values for ten plots.

(c) For 5-10 m tall individuals (the members of the low-stature tree layer), cover of each species was computed using the Dbh/crown cover regression equations (see Appendix 2). The total crown cover by species of all low-stature individuals rooted in a 6 x 100 m plot was computed and expressed as a percentage of the total plot area. The mean cover for low-stature tree species in the whole sample is based on cover values from forty 6 x 100 m segments on all four transects. These percentage cover values for the layer as a whole may be exaggerated because crown overlap was disregarded in the technique of cover computation.

Table 2 gives the cover distribution (%) by species in three height layers of the forest. The herbaceous plant species present on the four transect-profiles are listed first, followed by a listing of herbaceous plant species not occurring in the four transect-profiles, but present in the whole sample. The species listing under the two respective herbaceous plant species groups and the two taller forest layers is in order of quantitative importance in the whole sample. The cover of the herbaceous plant layer, varies from 19.5% on plot 1 to 33.1% on plot 20. The mean of the herbaceous plant cover in the four plots is very similar to the percent herbaceous cover over the whole sample. Twenty-six herbaceous plant species were encountered in the four plots. In addition, thirty-four other herbaceous plant species (i.e. a total of 60 species) were encountered in the whole sample area (10 plots). Of the herbaceous species present on the four plots, the sedge *Carex alligata*

Table 3

Stem Cover of Tree Species

LAYER Species	TRANSECTS	POINT-CENTERED QUARTER
EMERGENT TREE LAYER (>15 m tall)		
Acacia koa var. hawaiiensis	14.7 m^2/ha	15.0 m^2/ha
Acacia koa var. hawaiiensis snags	5.4 m^2/ha	2.1 m^2/ha
Metrosideros collina subsp. polymorpha	5.0 m^2/ha	1.4 m^2/ha
TOTAL	25.1 m^2/ha	18.5 m^2/ha
*INTERMEDIATE-STATURE TREE LAYER (10-15 m tall)		
Acacia koa var. hawaiiensis	0.1 m^2/ha	--
Metrosideros collina subsp. polymorpha	5.1 m^2/ha	--
TOTAL	5.2 m^2/ha	
*LOW-STATURE TREE LAYER (5-10 m tall)	6.3 m^2/ha	--
% Contribution by:		
Metrosideros collina subsp. polymorpha	53.6	--
Cheirodendron trigynum	25.2	--
Myoporum sandwicense	11.0	--
Ilex anomala	6.3	--
Coprosma rhynchocarpa	1.6	--
Myrsine lessertiana	1.6	--
Acacia koa var. hawaiiensis	0.5	--
Pelea volcanica	0.2	--
Pelea clusiaefolia	0.1	--
TOTAL	100.0	

*Individuals in the intermediate-stature and low-stature tree layers were not sampled by the point-centered quarter method.

the stem cover values are very similar. This indicates that _Acacia koa_ emergents were equally well sampled in the transect count and the point-centered quarter method. For _Acacia koa_ snags and _Metrosideros_, in the emergent layer, the stem cover values from the transect count are far greater than those obtained from the point-centered quarter method. This can be explained from the small sample of _Acacia koa_ snags and _Metrosideros_ emergents included in the point-centered quarter sample.

In the intermediate-stature tree layer, _Metrosideros_ had a higher stem cover than _Acacia koa_. _Metrosideros_ is more numerous than _Acacia koa_ in this layer. The total contribution of stem cover by individuals of _Metrosideros_ and _Acacia koa_ in the intermediate-stature tree layer is only about one-fifth that of the emergent tree layer.

The low-stature tree layer contributes a stem cover similar to that of the intermediate-stature tree layer. Nine species were enumerated in this layer. Of these, _Metrosideros_ contributes to over half the stem cover, _Cheirodendron_ contributes one-fourth of the stem cover and _Myoporum_ contributes just over one-tenth the stem cover of this layer. Three species (_Ilex_, _Coprosma_, _Myrsine_) could be considered minor stem cover components of the low-stature tree layer. _Ilex_ has a higher basal area than _Coprosma_ and _Myrsine_. The stem cover contributions by the three species _Acacia koa_, _Pelea volcanica_ and _Pelea clusiaefolia_ are rather insignificant.

Density relations of species in the different forest layers. — Fig. 11 shows the density (i.e. numbers) of woody plant species in the five forest layers. The curve slopes from left to right in the form of a straight line. There are nearly 21,600 individuals per ha in the

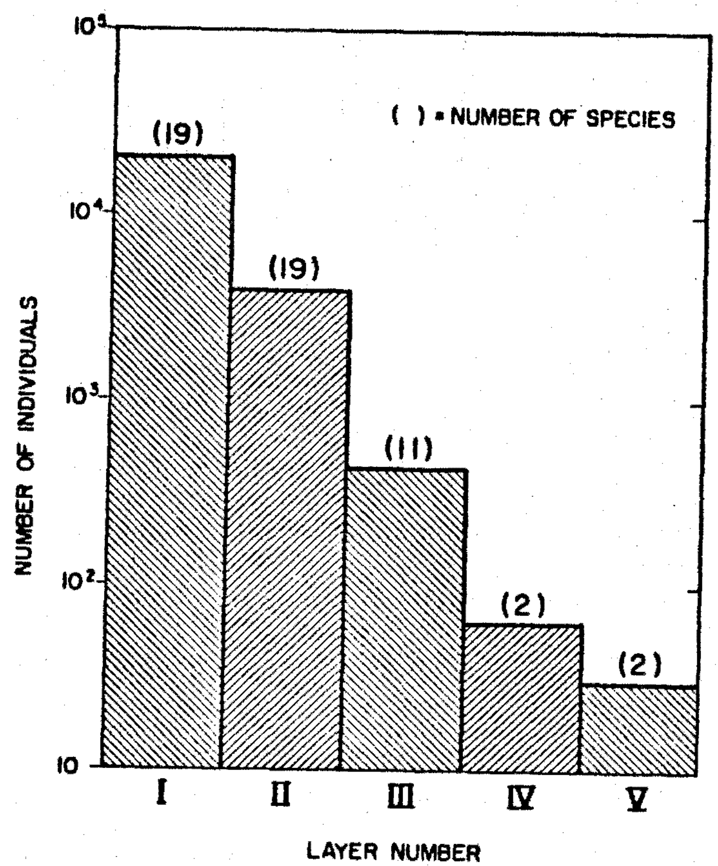


Fig. 11. Density of woody plants in the five forest layers on the basis of no./ha
I - Herbaceous plant layer (0-0.5 m tall)
II - Tree fern layer (0.5-5 m tall)
III - Low-stature tree layer (5-10 m tall)
IV - Intermediate-stature tree layer (10-15 m tall)
V - Emergent layer (>15 m tall)

herbaceous plant layer and just over 30 individuals per ha in the emergent tree layer. The herbaceous plant layer (0-0.5 m tall) contained 19 woody plant species and so did the tree fern layer (0.5-5 m tall). There were 11 species in the low-stature tree layer (5-10 m tall). Only two species, namely Metrosideros collina subsp. polymorpha and Acacia koa var. hawaiiensis, were found in the intermediate-stature (10-15 m tall) and the emergent tree layer (>15 m tall).

Table 4 shows the density of woody plants by species in the five forest layers. In Table 4, the species in the different height layers are listed in ranked order from species with high density to species with low density. Acacia koa is represented by relatively high numbers of individuals in the herbaceous plant layer (107.9/ha) as well as in the emergent layer (23.9/ha). The number of koa individuals in the tree fern, the low-stature and the intermediate-stature tree layers are rather low.

A more detailed breakdown of koa in size-classes is shown in Fig. 18 (page 91). Of the approximately 108 koa individuals in the 0-0.5 m herbaceous plant layer, about 91 are less than 10 cm tall and about 17 are in the height range from 10-49 cm (Fig. 18). Almost two thirds of the less than 10 cm tall koa individuals are root sprouts (62.9/ha). The rest are seedlings (28.3/ha). In the 10-49 cm reproduction class, there are less root sprouts (2.9/ha) than seedlings (13.8/ha). This indicates a greater mortality of root sprouts than of seedlings in the early stages of growth. Yet, approximately half the survivors that grow taller than 10 cm also seem to survive in the tree fern layer (0.5-5 m height). Koa saplings are reduced by a mortality factor when they reach into the tree fern layer. Of the approximately 17 koa individuals in the 10-49 cm reproduction class, only five grow taller into the 0.5-0.99 cm

Table 4

Density (Number of Individuals/ha) of Woody Species in the Five Height Layers

Species	Layer I (0-0.5 m)	II (0.5-5 m)	III (5-10 m)	IV (10-15 m)	V (>15 m)
Acacia koa var. hawaiiensis	107.9*	7.9	1.6	1.3	23.9
Metrosideros collina subsp. polymorpha	8,237.5	271.7	254.6	59.3	7.3
Cheirodendron trigynum	3,279.2	636.7	101.4	0	0
Ilex anomala	1,233.3	281.6	29.9	0	0
Myoporum sandwicense	25.0	21.7	17.7	0	0
Coprosma rhynchocarpa	441.7	33.3	10.4	0	0
Myrsine lessertiana	33.4	40.0	8.7	0	0
Alyxia olivaeformis	75.0	31.7	2.9	0	0
Pelea clusiaefolia	116.7	120.0	2.1	0	0
Pelea volcanica	45.9	11.7	1.2	0	0
Rubus hawaiiensis	1,266.7	60.0	0.8	0	0
Cibotium glaucum	16.7	2,486.6	0	0	0
Vaccinium calycinum	6,425.0	101.7	0	0	0
Broussaisia arguta	100.0	88.3	0	0	0
Cibotium chamissoi	+	21.7	0	0	0
Gouldia sp.	4.2	13.3	0	0	0
Rubus rosaefolius	154.2	6.7	0	0	0
Clermontia hawaiiensis	0	1.7	0	0	0
Cyrtandra lysiosepala	33.3	1.7	0	0	0
Cyanea sp.	8.3	0	0	0	0
Styphelia tameiameiae	4.2	0	0	0	0

+Small individuals (0-0.1 m stem-length) present but not enumerated due to problems of identification.

*For a finer breakdown of number of individuals by height classes see Fig. 18.

reproduction class (see Fig. 18). At this point, some mortality factor seems to become operative again, and of the five koa saplings in the 0.5-0.99 cm reproduction class, only approximately one grows over 1 m tall. This individual from then on has a good chance to grow into the emergent layer. Some mortality factor seems to become operative when koa saplings emerge from the tree fern into the low- and intermediate-stature tree layers. Here their number is reduced from about 8 per ha to 2 or 1 per ha. But in the emergent height class (>15 m tall), there are about 24 koa trees per ha, and these are undoubtably of different ages as they range in diameter from 35 cm to 175 cm (Fig. 18). Metrosideros collina is more abundant than Acacia koa in the four lower layers; it is represented by a large number of individuals (nearly 76 times as many individuals as Acacia koa) in the herbaceous plant layer and shows a successive decrease in the number of individuals with increasing height layers (Table 4). Metrosideros is well represented in all height layers and forms the numerically dominant species in the low-stature and intermediate-stature tree layers.

All species reaching into the low-stature tree layer (III, Table 4), show a successive decrease in density with increase in height layers except Myrsine lessertiana and Pelea clusiaefolia. Both Myrsine lessertiana and Pelea clusiaefolia have a slightly higher number of individuals in the tree fern layer (0.5-5 m tall) than in the herbaceous layer (0-0.5 m tall). This could reflect a high survival chance once seedlings of these species become established. Most of the species in the low-stature tree layer (III, Table 4) are tree species, but the woody vine Alyxia olivaeformis and the straggling shrub Rubus hawaiiensis also reach this layer. Metrosideros collina is the most abundant species in the low-stature tree layer. But among species whose height growth terminates in this layer, Cheirodendron trigynum is the most abundant.

The tree fern layer (II, Table 4), as the name implies, is dominated by the tree fern Cibotium glaucum. Small individuals (less than 0.1 m stem-length) of this species were present in the forest, but only a few were enumerated due to the problem of identification. This accounts for the relatively low density of Cibotium glaucum in the herbaceous plant layer (0-0.5 m tall). Small individuals (less tha 0.1 m stem-length) of Cibotium chamissoi were occasionally present, but not enumerated due to the problem of identification. Gouldia sp. has a greater density of individuals in the tree fern layer (II) than in the herbaceous plant layer (I), and so have Myrsine lessertiana and Pelea clusiaefolia. This could again reflect a high survival chance once seedlings of Gouldia sp. become established. One species in this layer (Clermontia hawaiiensis) had no 0-0.5 m stem-length individuals in the sample transects. This can be attributed to the rareness and the wide scatter of mature individuals of this species (1.7/ha in the tree fern layer) in the forest. Numerically, saplings of the low-stature tree species, Cheirodendron trigynum were next in abundance to Cibotium glaucum in the tree fern layer. Saplings of the tall tree species Metrosideros and saplings of the two low-stature tree species Ilex anomala and Pelea clusiaefolia also formed significant components of the tree fern layer.

Two species, Cyanea sp. and Styphelia tameiameiae were only present in the herbaceous plant layer. Both these species could potentially reach into the tree fern layer (0.5-5 m tall). But Styphelia is probably a relic species in this forest rather than an invader. Up to 1 m tall individuals of these two species were observed outside the sample transects. Metrosideros had the highest density of seedlings in the herbaceous plant layer. This species had an average of about 1 seedling every 1.5 m^2. These were clumped on logs and rotting wood. Next most abundant were seedlings of the shrub species Vaccinium calycinum, with an average of about one seedling per 2 m^2. Seedlings of Cheirodendron, Rubus hawaiiensis and Ilex were next in abundance in this layer.

Stand structure in terms of stem-length and diameter classes. — Fig. 12 shows the size-class distribution of individuals irrespective of species and without regard to strata.

The stem-length classes relating to woody plants up to 5 m tall show a left to right sloping curve from approximately 174,000 individuals per ha in the less than 1 m stem-length class to approximately 150 individuals per ha in the 4 to 4.99 m stem-length class.

Only trees > 5 m tall and >2.5 cm Dbh are included in the Dbh classes. The number of individuals by Dbh class also shows a generally left to right sloping curve. But the slope of this curve is somewhat irregular. It shows some plateauing. Also, the curve is interrupted by the absence of individuals in some size-classes. This type of curve pattern may be explained by the fact that not all species have the same growth potential in this forest. Many more species are represented in the smaller size-classes than in the larger size-classes. For this reason the stand structure curve (Fig. 12) cannot be treated as an age-class distribution curve. However, Fig. 12 indicates that there is good reproduction in the stand as a whole, and except for one species (Rubus rosaefolius), this is all of native woody species. Also, the slope of the size-class distribution curves indicates that the stand is maintaining itself.

A more detailed assessment of the forest structure can be obtained

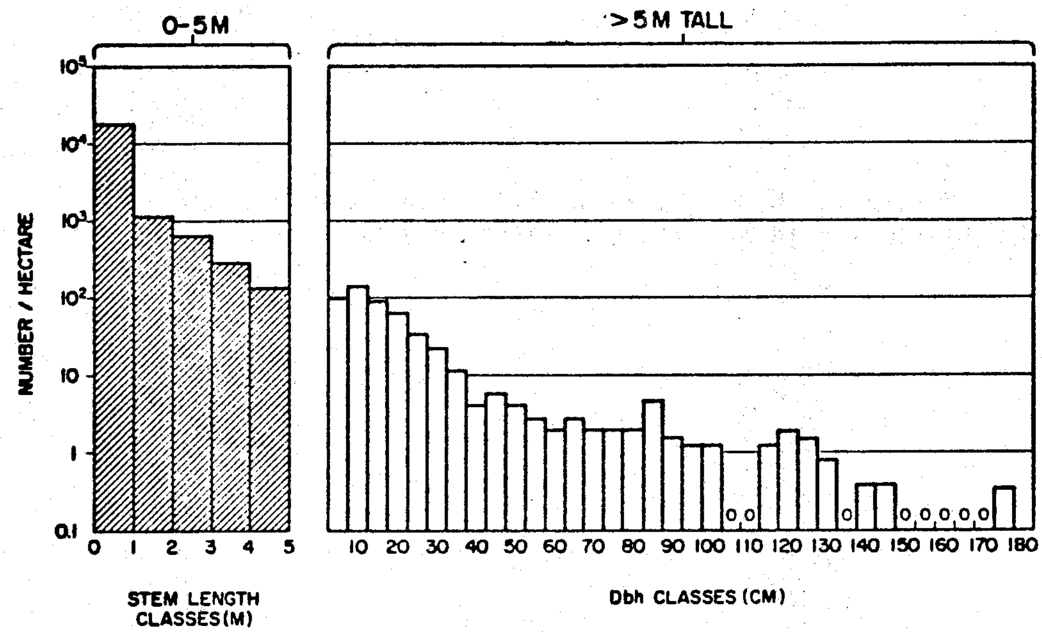


Fig. 12. The frequency distribution of all woody plants in the stand in stem-length and diameter at breast height (Dbh) classes.

through an evaluation of individual species population structures.

Population structure of woody plant species

Twenty-one woody plant species were enumerated in the transects. Of these, two tree ferns and ten other woody plant species formed the components of the tree fern layer. Seven low-stature tree species and two tall tree species were recorded.

Species in the tree fern layer (< 5 m tall). — The twelve species enumerated in this layer can be classified into three structural similarity groups:

1. Species with uninterrupted presence in all stem-length classes. — These are the four species shown on Fig. 13, and include the tree fern *Cibotium glaucum*, the tall shrub *Broussaisia arguta*, and straggling thin branched shrub *Rubus hawaiiensis* and the thin-stemmed woody vine *Alyxia olivaeformis*. All four species have their largest number of individuals in the lowest stem-length class of less than 1 m with gradually decreasing individuals in the larger stem-length classes. This indicates a high stability potential for these species in the stand. The most steady replacement pattern with increasing size is indicated by *Cibotium glaucum* and *Broussaisia*, while *Rubus hawaiiensis* and *Alyxia* show a greater reduction in number of individuals in the second stem-length class (1-1.99 m stem-length). This indicates a relatively greater mortality for individuals of the latter two species when they grow above 1 m stem-length in size. However, those that survive have a greater chance of maintaining themselves to the maximum size potential, which is indicated by the relatively uniform number of individuals found in the stem-length classes over 1 m.

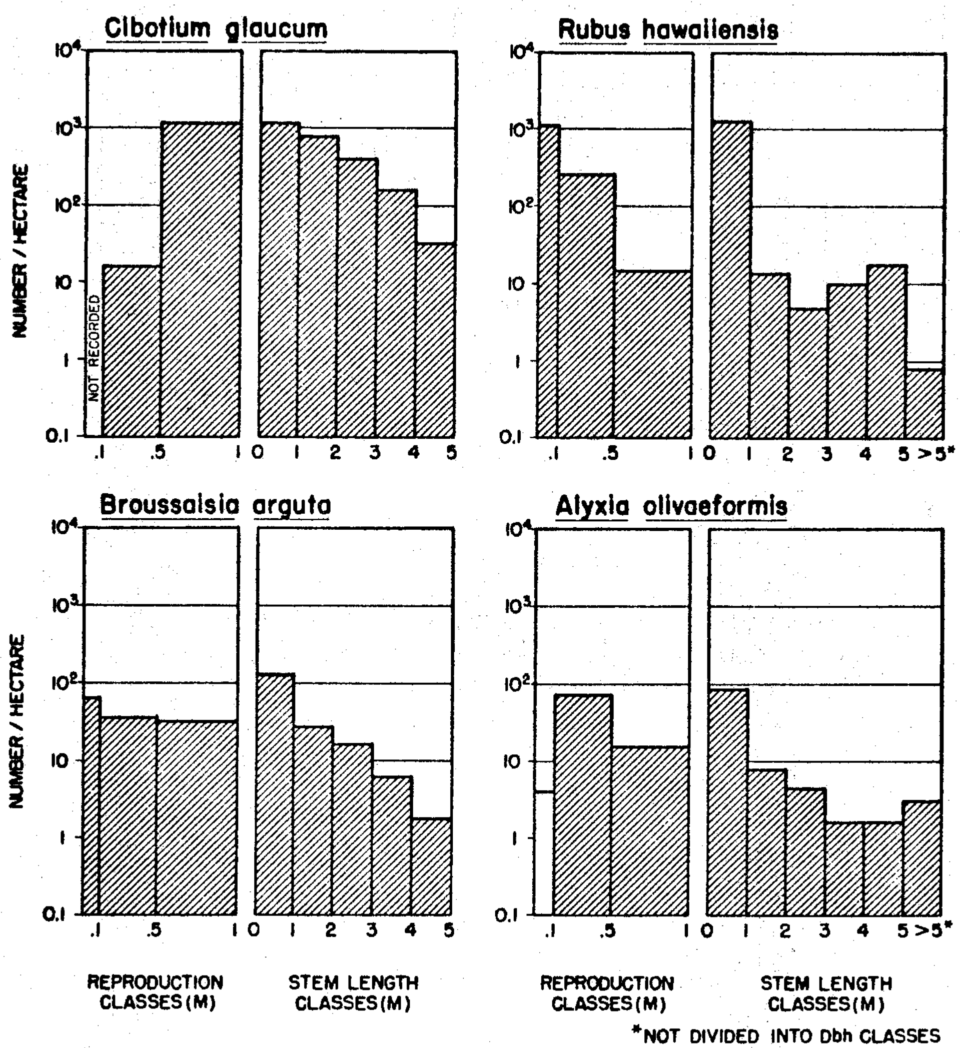


Fig. 13. Population structures of species in the tree fern layer (< 5 m tall) with uninterrupted presence in all stem-length classes.

The distribution of individuals in the less than 1 m stem-length class is further detailed in three reproduction-classes for each species (see left-side diagrams on Fig. 13). The numerical distribution of these smaller individuals supports the stability trends recognized for the taller individuals, i.e. there are usually as many or more smaller sized individuals than larger sized ones per unit area for _Broussaisia_, _Rubus hawaiiensis_ and _Alyxia_. An exception is shown for _Cibotium glaucum_. Individuals under 10 cm height of this tree fern were not recorded because of identification problems. The smaller number of individuals in the 0.1-0.49 m stem-length class (12/ha) as compared to the 0.5-0.99 m stem-length class (over 300/ha) does not really reflect a beginning disruption in the reproduction process for this species. It is rather a reflection of the peculiarity of early growth and the reproduction mode of this species. Many small tree ferns seem to arise from lateral buds of older stems. By the time they can be recognized as distinct individuals, they are usually already longer than 0.5 m.

The diagrams also indicate the magnitude of numbers for these species. They show that _Cibotium glaucum_ and _Rubus hawaiiensis_ individuals are represented with over 1,000 individuals/ha in the less than 1 m stem-length class, while _Broussaisia_ and _Alyxia_ individuals number about 100/ha in the same stem-length class.

2. _Species with individuals absent in some stem-length classes_. — These include three species in the tree fern layer (_Cibotium chamissoi_, _Cyrtandra lysiosepala_ and _Clermontia hawaiiensis_) (Fig. 14). The distribution of individuals among the stem-length classes shows that for _Cibotium chamissoi_ and _Cyrtandra_ there are more individuals in the less

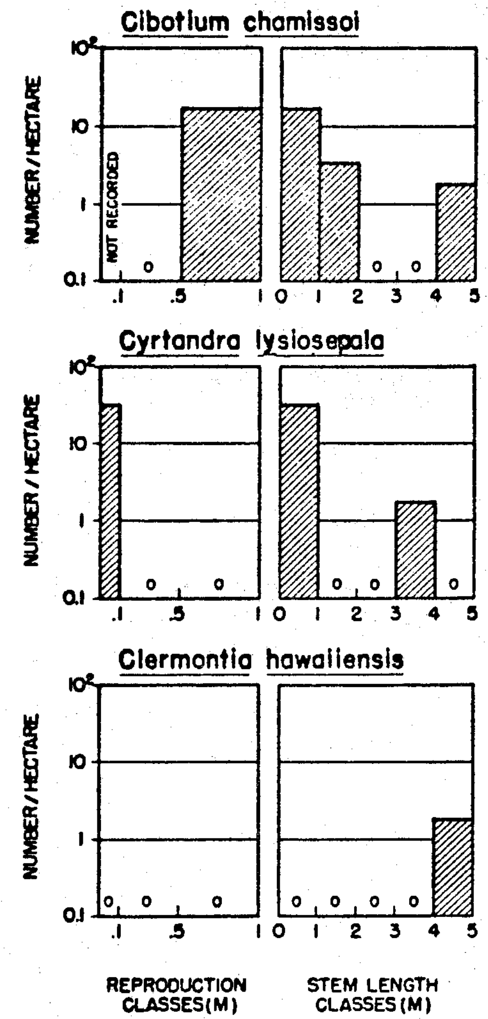


Fig. 14. Population structures of species in the tree fern layer (< 5 m tall) with individuals absent in some stem-length classes.

than 1 m than in the higher stem-length classes. This trend is similar as in the previously discussed group. However, the number of individuals per hectare is very much smaller (by a factor of 10) for the species in Fig. 14, and their generally low abundance can account for the absence of individuals in some size-classes. An extreme case is Clermontia hawaiiensis, of which individuals of only 4-4.99 m stem-length were recorded. Since there were only about two individuals per hectare encountered in the sample, the absence of individuals in other classes can be attributed to the wide scatter of this species in the forest. A definite trend for this species can only be ascertained from a much greater area sample.

3. Species with individuals present only in the lower stem-length classes. — This group includes the five species (Vaccinium calycinum, Gouldia sp., Rubus rosaefolius, Styphelia tameiameiae, Cyanea sp.) shown in Fig. 15. The first two species are represented in more than one stem-length class, while the remaining three are represented with individuals in only the lowest class. This distribution trend merely indicates that these five species reach their stem-length potential at smaller size. They are thus the smaller members of the tree fern layer. The reproduction-classes show a definite stability trend for Vaccinium calycinum and Rubus rosaefolius. Styphelia and Cyanea are represented only by seedlings and small plants in this forest. For Styphelia, which is a seral species growing abundantly on certain lava flows, this indicates a relic rather than a pioneering position in this forest, while for Cyanea, which is a shade plant found in dark rain forests, this indicates establishment by seedlings. The reproduction size-class trend of Gouldia may indicate that this species could become still rarer in the future.

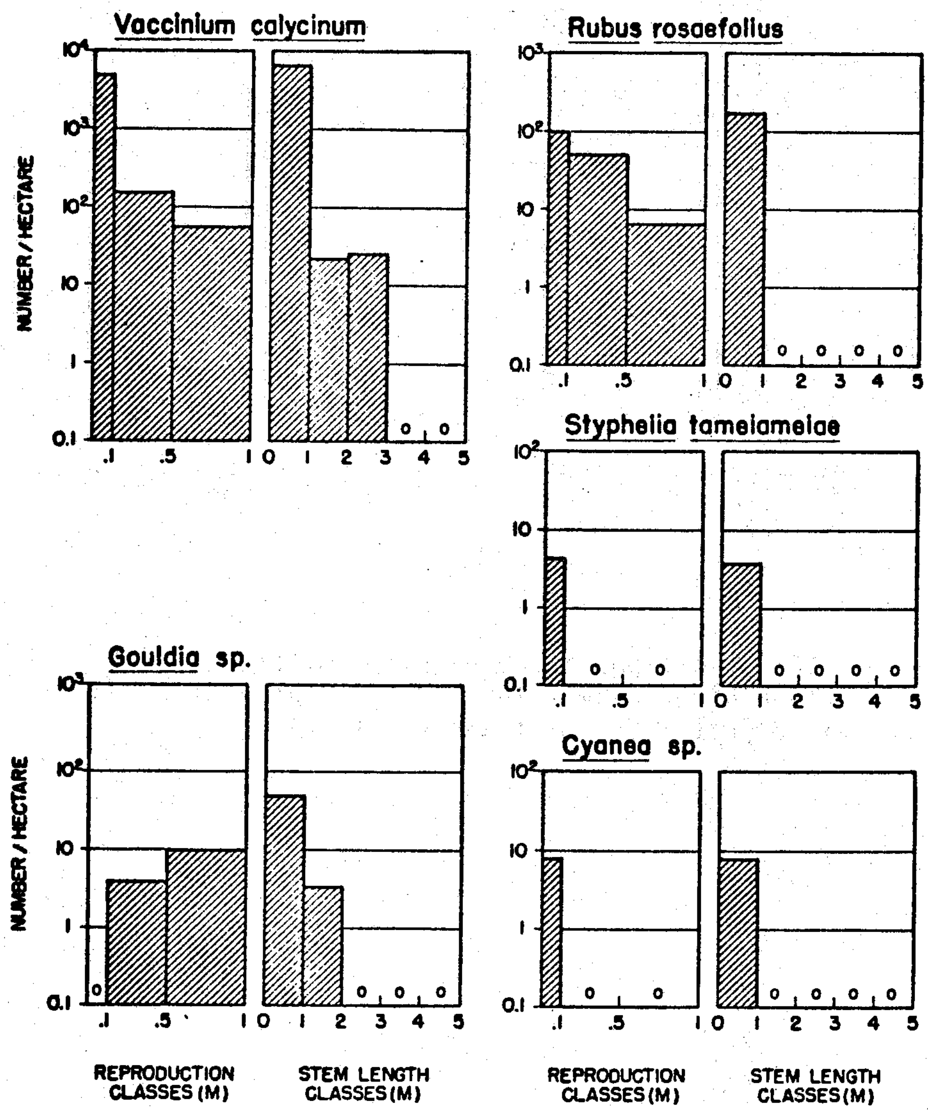


Fig. 15. Population structures of species in the tree fern layer (< 5 m tall) with individuals present only in the lower stem-length classes.

Low-stature tree species. — The seven species enumerated in this layer can be classified into two structural groups:

1. Species with uninterrupted presence in all size-classes. — This group includes three species (*Cheirodendron trigynum*, *Coprosma rhynchocarpa*, *Pelea clusiaefolia*) which are represented in Fig. 16. All three show strong stability trends, by being represented with large numbers of seedlings and a reasonable number of saplings (i.e. individuals in the 1 m to 4.99 m stem-length classes), as well as mature individuals. The numerical distribution by size-class follows an inverse J-shaped curve trend (if their numbers were plotted on ordinary graph paper), in almost all size subdivisions.

In addition, the diagrams on Fig. 16 show abundance differences between the species. *Cheirodendron*, which is the most abundant of the tree species in this structural group, is also the one with the greater diameter growth potential, here growing into the 35 cm Dbh class.

2. Species with individuals absent in some size-classes. — This group includes four native tree species (*Myoporum sandwicense*, *Ilex anomala*, *Myrsine lessertiana* and *Pelea volcanica*) shown in Fig. 17. The numerical distribution by size-classes for three of the species in this group, namely, *Ilex*, *Myrsine* and *Pelea volcanica*, generally follows a left to right sloping curve. The Dbh size-class distribution of *Myoporum* is skewed and shows a peak at the 15 cm Dbh class. This may reflect rapid initial diameter growth in *Myoporum*.

The diagrams in Fig. 17 also show abundance differences between the species with *Ilex* being the most abundant and *Myoporum*, *Myrsine* and *Pelea volcanica* being less abundant. The number of individuals per

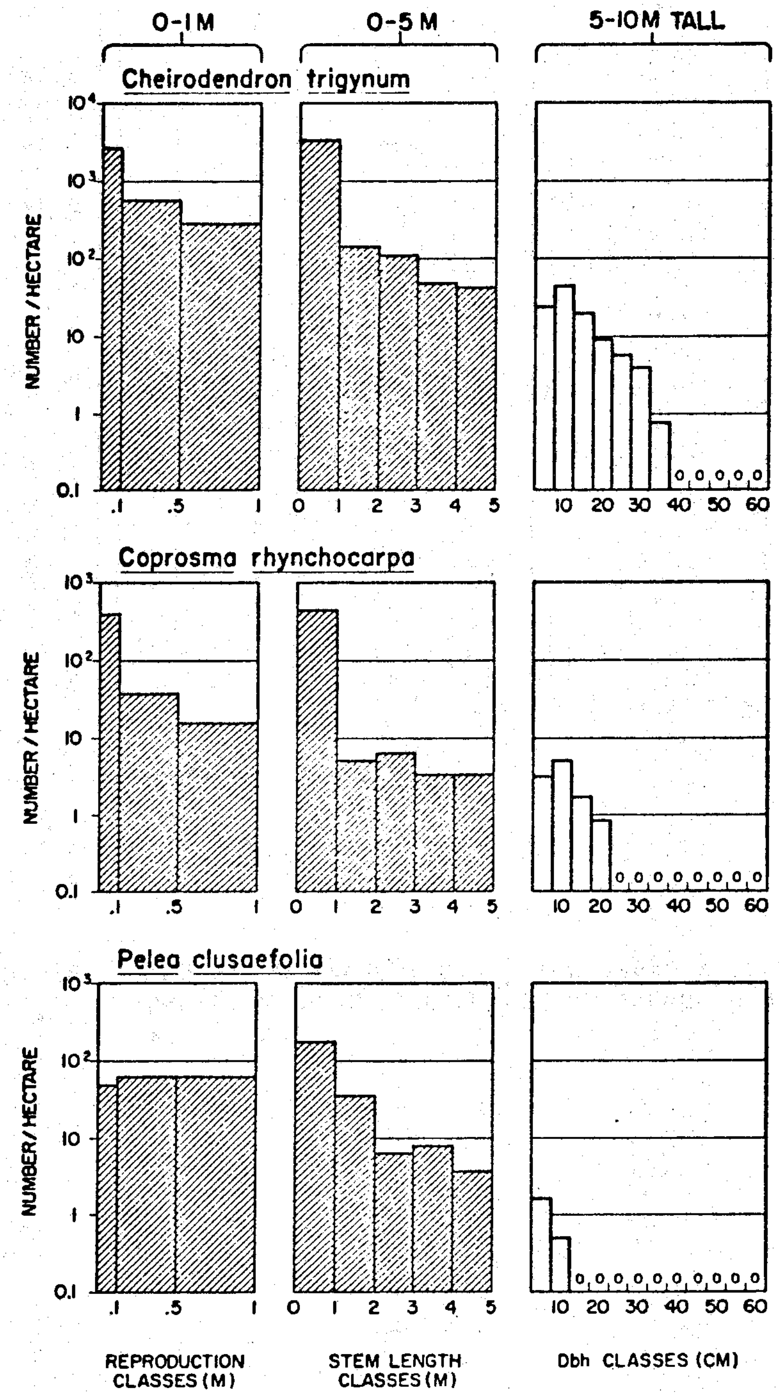


Fig. 16. Population structures of low-stature tree species with uninterrupted presence in all size-classes.

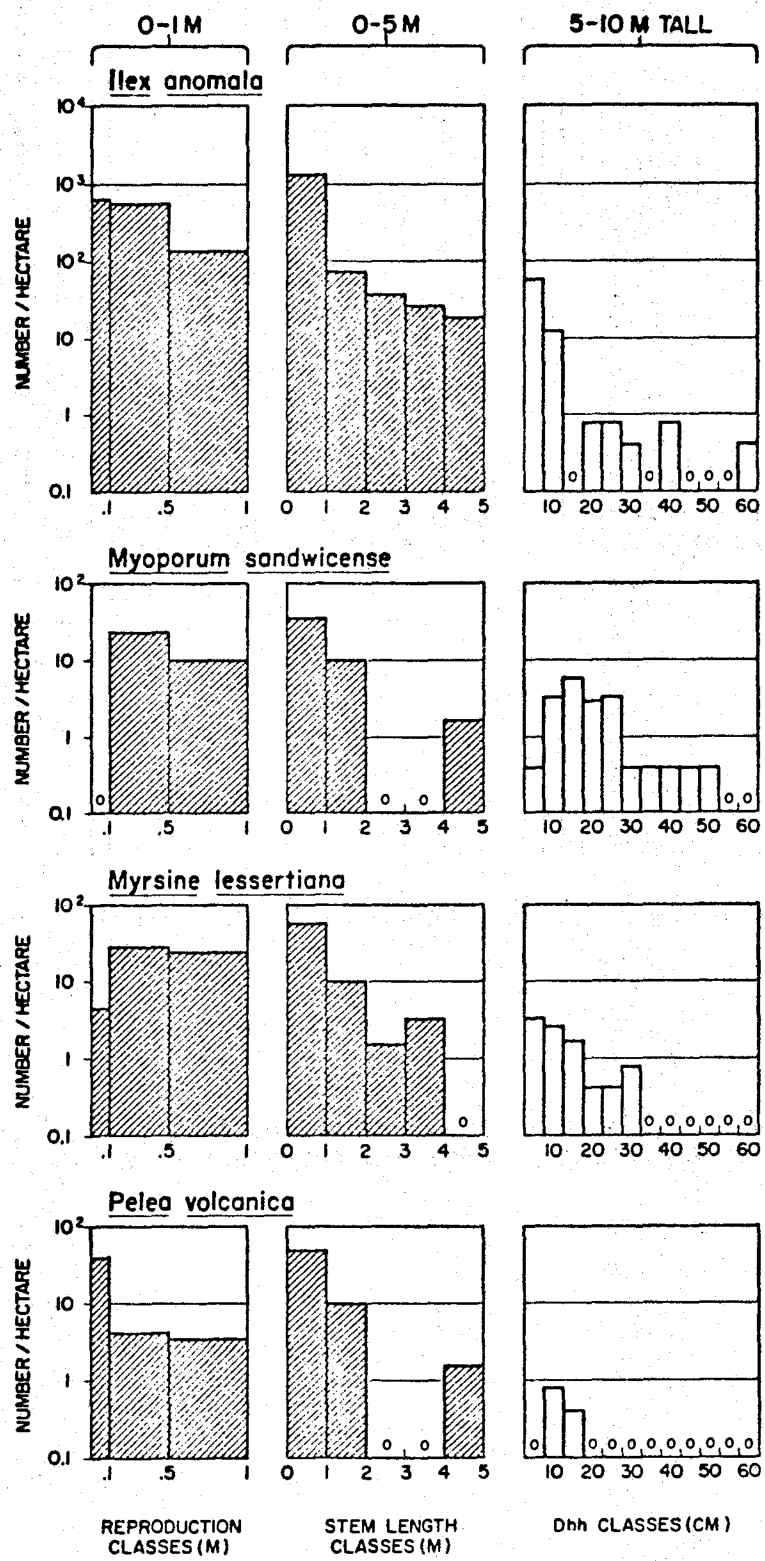


Fig. 17. Population structures of low-stature tree species with individuals absent in some size-classes.

hectare of Ilex is high and comparable to that of species in the previously discussed low-stature tree group. The number of individuals per hectare of the three other species in this group are much smaller, and their generally low abundance can account for the absence of individuals in some size-classes. The stem-length size-class distribution of Ilex shows a continuous replacement pattern, but the Dbh size class distribution shows interruptions. These interruptions may reflect periodic disturbances in seedling establishment of this species in the past.

Of the four species in this group, Ilex also has the greatest diameter growth potential, here growing to 60 cm Dbh. Myoporum has a diameter growth potential somewhat similar to but less than that of Ilex. Of the two species of Pelea in this forest, Pelea volcanica seems to have greater diameter growth potential (Fig. 17) than Pelea clusiaefolia (Fig. 16).

Tall trees (> 10 m tall). — The distribution of individuals by size-classes of the two tall tree species (Metrosideros collina subsp. polymorpha and Acacia koa var. hawaiiensis) are shown in Fig. 18. In Metrosideros, the distribution of individuals in the reproduction classes and the Dbh classes show curves sloping from left to right. This shows a high stability-potential for this species. A very large number (8,465.8/ha) of Metrosideros individuals are found in the below 1 m stem-length class, but there is a considerable reduction in the number of individuals in subsequent stem-length classes of this species (Fig. 18). This suggests a high seedling mortality in the early stage of growth in this species.

Acacia koa clearly reproduces in the forest stand (Fig. 18). This

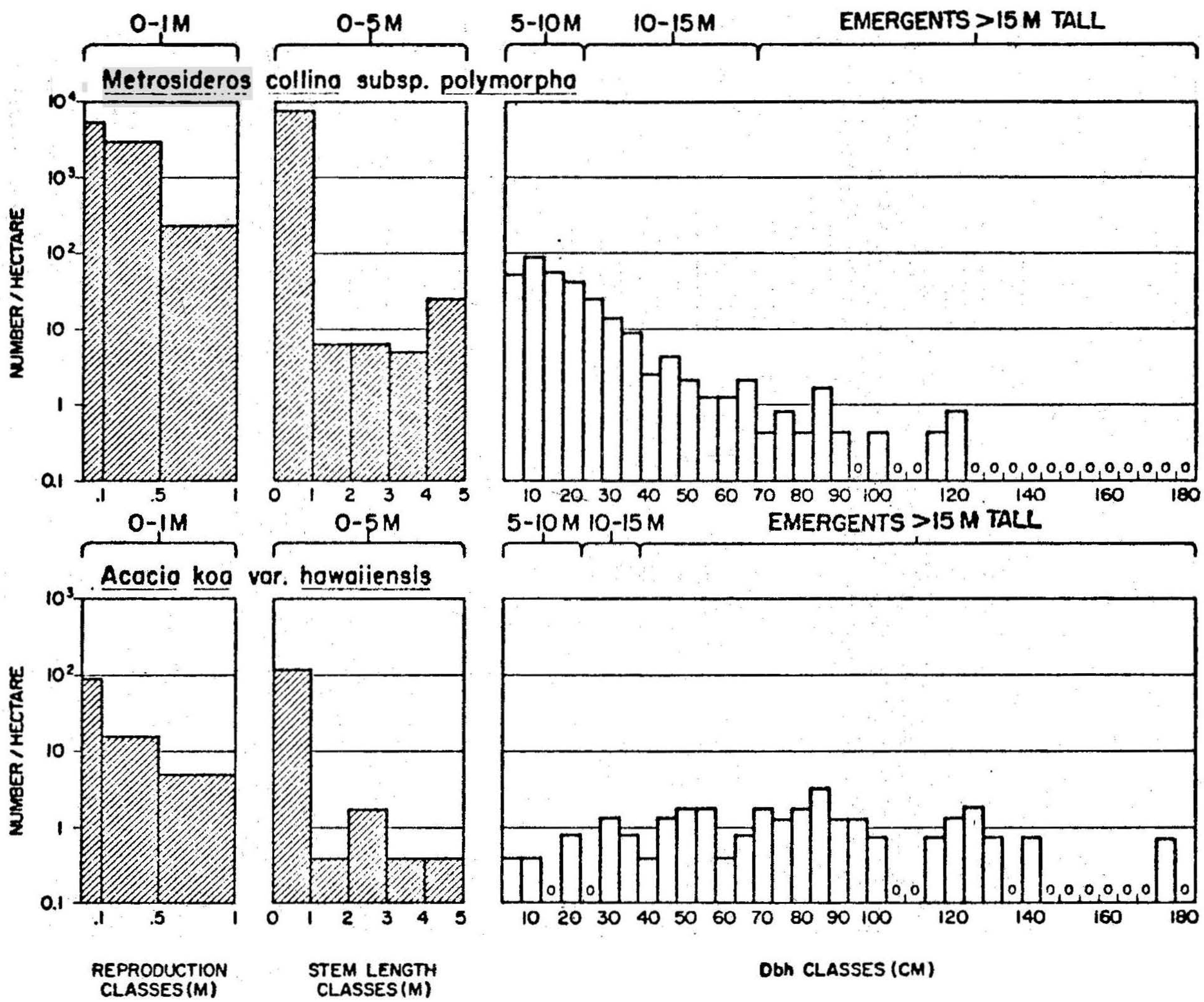


Fig. 18. Population structures of the two tall tree species.

species is represented in all stem-length and reproduction-size classes. There is a considerable reduction in the number of individuals from the less than 1 m stem-length class to the 1-1.99 m stem-length class. This reduction is similar to the trend in Metrosideros. However, seedlings of Metrosideros in the below 1 m stem-length class are of greater abundance (by a factor of 80) than Acacia koa individuals in the same stem-length class. The distribution of Acacia koa individuals in the Dbh size-classes does not follow a curve sloping from left to right seen in Metrosideros. The curve shape for Acacia koa resembles more or less a plateau with several dips and crests. The density of individuals in the lower Dbh classes are similar to the density of individuals in the larger stem-length classes. This suggests that even though early seedling mortality is high, Acacia koa saplings once established are continuously recruited into the tree layers. Height growth of Acacia koa is more rapid than in Metrosideros. In Fig. 18, 35 cm Dbh Acacia koa individuals reach the emergent (>15 m) stature, whereas Metrosideros individuals reach the emergent stature only when they are about 65 cm Dbh in size. Acacia koa also has a greater diameter growth potential than Metrosideros, and here grows to 175 cm Dbh.

Snags. — The dead-standing trees include Acacia koa, Metrosideros and unidentified snags. Their distribution trends by size classes are represented in Fig. 19. The pattern for Acacia koa snags is similar to that of the live trees of this species. But snags are more abundant in the 30 cm to 80 cm Dbh classes than in the lower or higher Dbh classes. This suggests that more tree mortality occurs in this Dbh range.

Snags of Metrosideros collina were found only in the lower Dbh classes (Fig. 19). The largest snags of Metrosideros were in the 35 cm

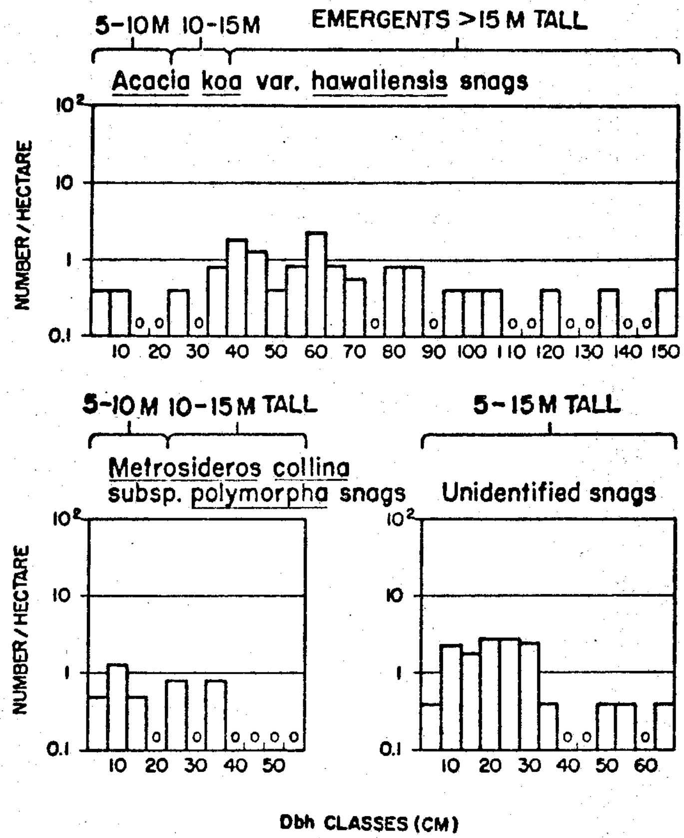


Fig. 19. Size-class distribution of snags.

Dbh class. The absence of Metrosideros snags in larger Dbh classes may be due to more rapid breakdown of the larger snags of this species.

Snags that could not be identified were grouped into one group (Fig. 19). This group shows a high density of snags in the smaller Dbh classes. This group may thus be comprised largely of low-stature tree species.

Log and soil distribution of tree species

During the survey, it was observed that many seedlings of tree species were growing on logs. Moreover, it was also observed that many trees over 5 m tall also showed signs of having become established on logs. These were defined as log-established trees. They include (1) trees that are on logs, with their roots not yet reaching the mineral soil (Fig. 20), (2) trees on logs with their roots reaching the mineral soil (Fig. 21), and (3) trees which indicate by their present root system that they once started on logs (Fig. 22). The latter trees have prop roots which hold the stem-base of the tree above ground level. In this case, the logs that once served as substrates have decayed (Fig. 22). Tree types (2) and (3) are now rooted in the mineral soil, but they differ in appearance from normally soil-rooted trees which start with their trunk base on the mineral soil. Trees of this latter type were defined as "soil established" because they probably germinated directly on the forest floor.

A species index for log-established trees. — A simple expression for the degree of log-establishment of a species is the "log-establishment index" (LEI), which is calculated as the log-established individuals divided by the total individuals expressed as a percentage (i.e.

Fig. 20. Epiphytic Cheirodendron trigynum (20 cm Dbh) rooted on Metrosideros 3.5 m above ground. C. trigynum becomes established preferentially on logs and tree trunks but is not an obligate epiphyte. (Scale 1:40)

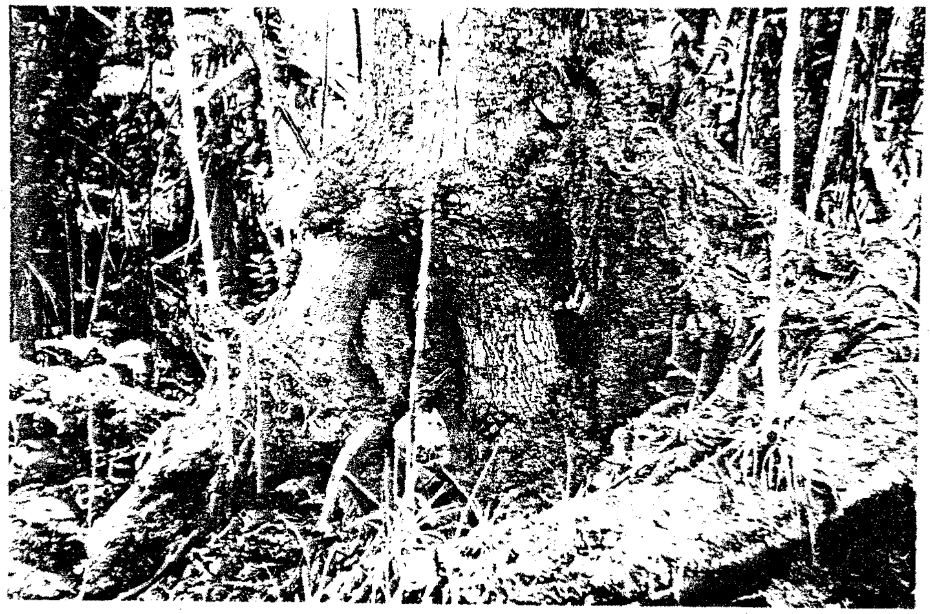


Fig. 21. Prop roots of Acacia koa var. hawaiiensis tree which had germinated on a root collar. The root collar had decayed, but the tree trunk is still partially embedded between the prop roots. (Scale 1:25)

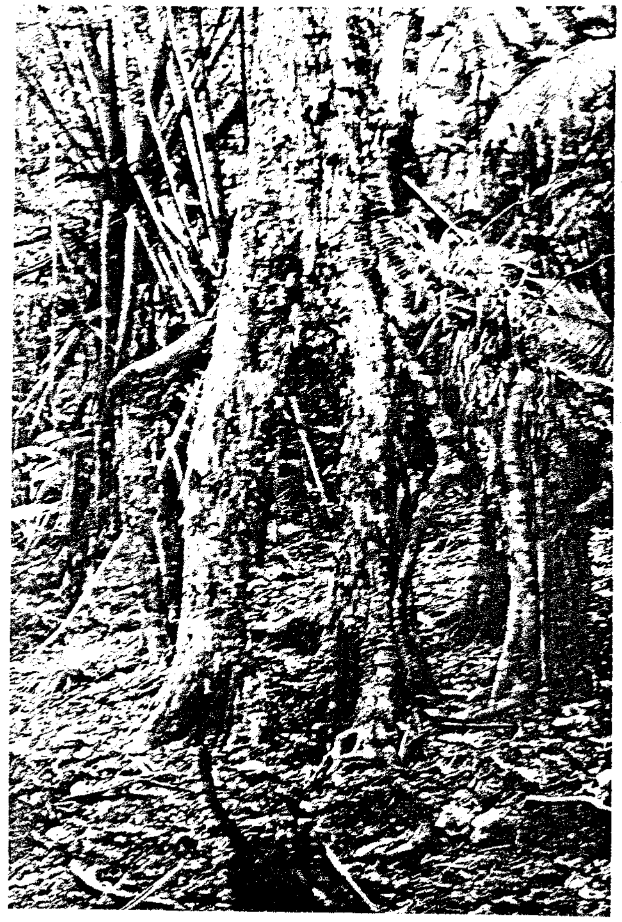


Fig. 22. Metrosideros collina subsp. polymorpha tree established as epiphyte. The log on which the tree became established had decayed, leaving the tree to support itself on its prop roots. (Scale 1:20)

$\text{LEI} = \frac{\text{No. of individuals log-established}}{\text{Total no. of individuals of that species}} \times 100$). Theoretically the LEI of a species could range from 0%, meaning no individual of that species was established on logs, to 100%, where all individuals were log-established.

The LEI's for all low-stature and tall tree species are shown in Table 5. These LEI's are based on actual counts of trees >5 m tall and ⩾2.5 cm Dbh in a 2.4 hectare area. The two tall tree species and their snags and all low-stature tree species except *Myoporum sandwicense* and *Pelea volcanica* have LEI values of over 50%. This shows that logs as a tree germination and establishment medium are of considerable importance for the majority of the tree species in this forest. Other species of woody plants that were not recorded here, but would also show a low degree of log-establishment are the *Cibotium* species.

The LEI's in Table 5 can be considered reliable only for species with a large number of individuals, which, for practical purposes, have been considered to be a total of at least 20/2.4 ha or 8/ha. On the basis of this criterion, the LEI of *Pelea clusiaefolia*, *Pelea volcanica* and *Metrosideros* snags may not be considered reliable because of the small numbers of individuals counted. The LEI's of all other species and koa snags may be considered reliable. In the latter group, *Ilex* and *Cheirodendron* show very high LEI's. *Cheirodendron* sometimes grows as an epiphyte on live trees and then has the life-form similar to that of a strangling *Ficus* (Fig. 20). *Metrosideros* has an LEI which is about 10% higher than that of *Acacia koa*.

Most tree species are significantly log-established. — Table 6 shows the mean ground cover along transects 1 and 4. It shows that the

Table 5

Log-Establishment Indices for Tree Species

Species	Log-established / Total individuals	Percentage of log-established trees (LEI)
Low-stature tree species		
Ilex anomala	67/72	93.06
Cheirodendron trigynum	222/243	91.36
Pelea clusiaefolia	04/05	80.00*
Myrsine lessertiana	15/21	71.43
Coprosma rhynchocarpa	15/25	60.00
Pelea volcanica	01/03	33.33*
Myoporum sandwicense	05/43	11.63
Tall-tree species		
Metrosideros collina subsp. polymorpha	560/771	72.63
Metrosideros collina subsp. polymorpha snags	06/09	66.67*
Acacia koa var. hawaiiensis	40/64	62.50
Acacia koa var. hawaiiensis snags	19/33	57.58

*These indices are not considered reliable, due to the small number (less than 20/2.4 ha) of individuals enumerated.

Table 6

Mean Ground Cover along Transects 1 and 4 (from Ten 6 x 100 m Plots)

Cover	%
Rotting wood and lying logs	24.0
Exposed soil	71.9
Rocks	4.1
Herbaceous and bryophyte cover*	26.7

*Bryophytes cover much of the rotten wood and lying logs.

current ground cover on the forest floor is only 24% covered with logs, the rest (76%) is covered by mineral soil and rocks.

If it is assumed that seeds of tree species were distributed over the ground area by chance, and if it is also assumed that germination, establishment and subsequent survival of trees is only related to the position and not to the nature of the substrate, it could be expected that the ratio of log-established to soil-established individuals should be proportional to the log to soil covered area. It was seen in Table 6 that only 24% of the ground was covered by logs and rotting wood. If the foregoing assumptions are correct one would expect to find a greater soil-establishment of trees in the forest.

To test the null hypothesis of a 24:76 log-established to soil-established tree ratio, chi-square values were computed for all tree species, except the numerically inadequately sampled species, (i.e. *Pelea clusiaefolia*, *Pelea volcanica*, and *Metrosideros* snags). The chi-square values obtained are shown in Table 7. This table shows that all tree species, except *Myoporum sandwicense* were significantly log-established. Thus, establishment on logs has greater survival value for most tree species in this forest. *Myoporum* is a pioneer species in secondary succession. In the forest, it mostly occurs in forest openings. The two *Cibotium* species (not recorded here) are not pioneer species but are also mostly rooted on mineral soil.

The LEI of individual tree species sufficiently explains the log-establishment characteristics of all size-classes combined. But this value does not indicate possible changing trends in log-establishment within a population. For example, two species may have similarly high

Table 7

Chi-Square Values Obtained by Testing the Null Hypothesis of a 24:76 Log-Establishment:Soil Establishment Ratio for Tree Species

Species	X^2
Metrosideros collina subsp. polymorpha (5 cm-40 cm Dbh classes)	890.36**
Cheirodendron trigynum	601.05**
Ilex anomala	184.17**
Acacia koa var. hawaiiensis	49.66**
Myrsine lessertiana	23.69**
Acacia koa var. hawaiiensis snags	18.70**
Coprosma rhynchocarpa	15.84**
Myoporum sandwicense	2.94

**Significant at P = 0.01, df = 1.

LEI values due to different reasons. In one case it may be due to the presence of a consistently high number of log-established trees in all size-classes, with similar log-established:soil-established tree ratios in all size-classes. In another case it may be due to the presence of a large number of log-associated individuals in only a few size-classes. Recognition of such trends within the population are important to evaluate species maintenance patterns. Because of this, an analysis was made to identify trends within tree species populations.

Testing log-establishment:soil-establishment ratios with change of size within species. — To test the log-establishment:soil-establishment ratios with change in size within species, a heterogeneity chi-square (ΣX^2) test was made of all tree species in the following manner:

For each species, beginning with the lowest size-class (5 cm Dbh class), X^2 was calculated for each successive Dbh class provided the expected number of individuals for log-established and soil-established individuals was at least 1. If a Dbh class had an expected number of less than 1, successive Dbh classes were pooled till an expected number of at least 1 was obtained, and then X^2 was calculated for the pooled class. Because of this, the number of Dbh classes included in a pooled class may vary from species to species and from one pooled class to another within the same species. The groupings of 5 cm Dbh classes under each pooled class for heterogeneity chi-square (ΣX^2) computations for tree species is given in Appendix 1.

An attempt was made to compute the ΣX^2 for all tree species listed in Table 5. The sample size of *Pelea clusiaefolia*, *Pelea volcanica* and *Metrosideros* snags were inadequate to get expected values of at least

1 for log-established and soil-established individuals. This supports the cut-off point used for considering a log-established index as non-reliable, when less than 20 individuals were enumerated in the total sample (Table 5).

Table 8 shows the chi-square (X^2) values for pooled classes and the heterogeneity chi-square (ΣX^2) for eight tree species and _Acacia koa_ snags. The significance of the ΣX^2 values were tested using the method described by Snedecor and Cochran (1971) with df = (r - 1)(c - 1), where df = degrees of freedom, r = number of pooled classes and c = number of attributes (here two, soil-established and log-established). Only _Metrosideros_ and _Myrsine_ showed significant ΣX^2 values (see Table 8). A significant ΣX^2 suggests that the population is not represented by a common population of ratios. Instead, there is significant heterogeneity between the pooled class ratios which is not due to chance. The remaining species in Table 8, do not show significant heterogeneity between ratios, and the differences in their pooled-class ratios is likely due to chance.

In Table 8, all _Metrosideros_ individuals in Dbh classes $\geqslant$ 45 cm Dbh (all log-established) were included in pooled class 9. This pooled class has a X^2 of 14.57, the highest X^2 for any pooled class. A separate ΣX^2 test made for pooled classes 1 to 8 (Table 8) showed ΣX^2 not to be significant. Consequently, the differences in pooled classes 1 to 8 are due to chance. The high X^2 value for pooled class 9 accounts for the highly significant ΣX^2 value for _Metrosideros_. This implies that from 45 cm Dbh class on, the survival of log-established individuals is significantly greater than that of soil-established individuals of _Metrosideros_.

Table 8

Chi-Square (X^2) Values for Pooled Size-Classes and Heterogeneity Chi-Square (ΣX^2) for Tree Species

SPECIES	X^2 for pooled classes									ΣX^2
	1	2	3	4	5	6	7	8	9	
Metrosideros collina subsp. polymorpha	0.001	4.35	0.30	0.96	1.43	3.03	0.70	0.31	14.57	25.831**
Metrosideros collina subsp. polymorpha	0.10	2.43	0.001	0.39	2.07	3.62	1.02	0.40	--	10.031^{+}
Myrsine lessertiana	2.75	4.45								7.20*
Acacia koa var. hawaiiensis snags	0.12	1.89	0.58	1.54						4.13
Acacia koa var. hawaiiensis	0.27	0.28	0.09	0.40	1.07	1.19				3.30
Coprosma rhynchocarpa	0.02	1.13	1.78							2.93
Cheirodendron trigynum	0.11	0.08	0.27	0.39	0.03	0.0				0.75
Ilex anomala	0.15	0.16								0.31
Myoporum sandwicense	0.11	0.08								0.19

**Significant at P = 0.01 with d.f. = (no. of pooled classes-1)(2-1)
*Significant at P = 0.05 with d.f. = (no. of pooled classes-1)(2-1)
$^{+}\Sigma X^2$ for pooled classes 1 to 8 in Metrosideros. This value is not significant at P = 0.05, d.f. = 7. See Fig. 35 and text for further explanation.

Fig. 23 shows the percent log-establishment of Metrosideros and Myrsine by Dbh size-classes. The curve for Metrosideros (Fig. 23) when extrapolated gives a value of about 85% for log-established seedlings. This agrees with the observation that the greater proportion of Metrosideros seedlings are found on logs. The few Metrosideros seedlings rooted on mineral soil were generally found in "gap-areas."

The within species variation of log-establishment indices shows that intermediate-sized (10-20 cm Dbh) Metrosideros trees and intermediate-sized (15 cm Dbh) Myrsine trees are relatively more frequently soil-established compared with small trees and large trees of these two species.

Seedlings of Metrosideros and Myrsine rarely get established on mineral soil in the dense forest. However, seedlings of these two species may get established on mineral soil in areas where there are canopy gaps ("gap-areas"). The Metrosideros and Myrsine individuals established on mineral soil must have become established during disturbances which created canopy gaps. This suggests that the mineral soil established individuals may be "gap-phase" trees.

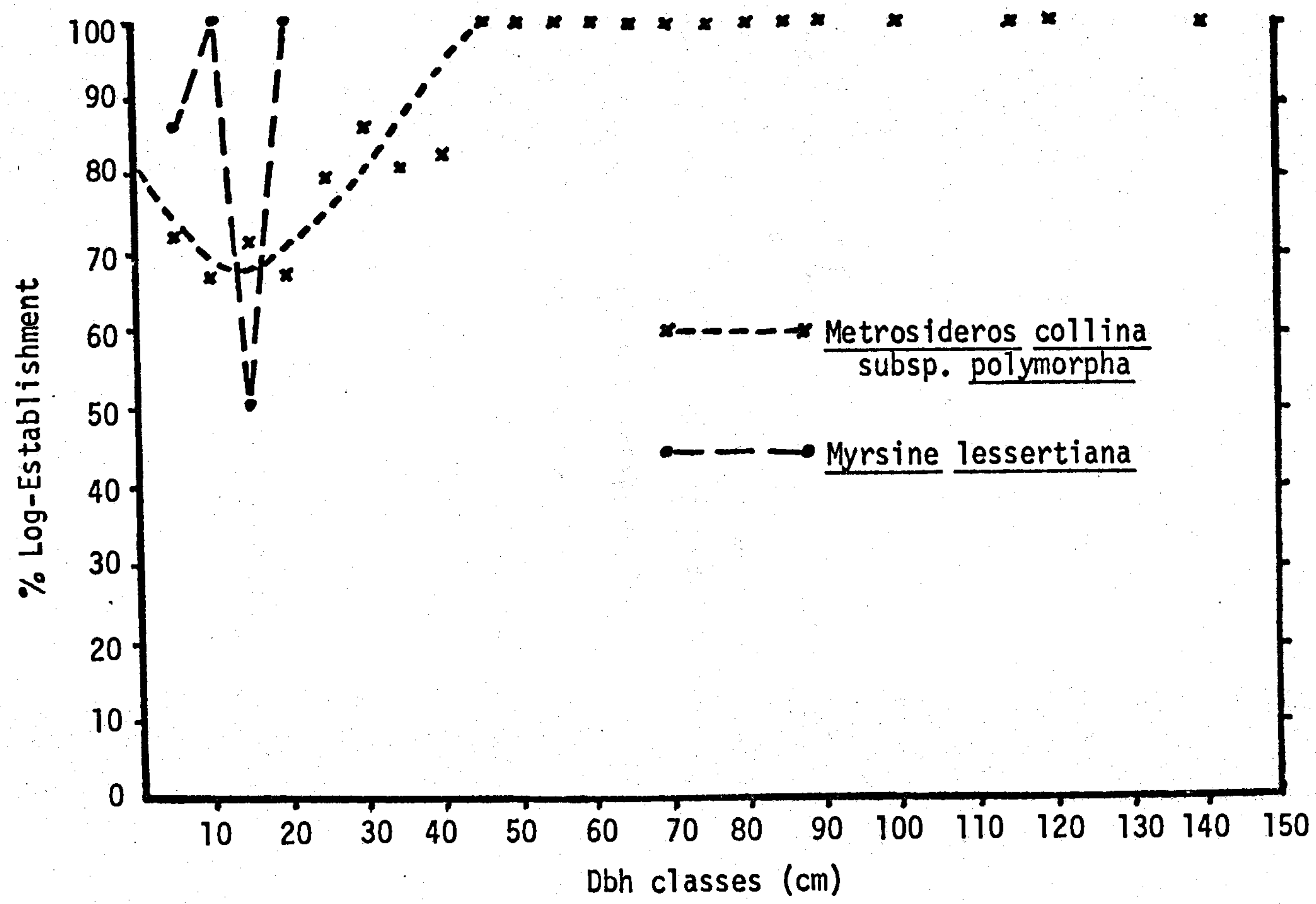


Fig. 23. Percentage log-establishment in Dbh classes of *Metrosideros* and *Myrsine*.

DISCUSSION AND CONCLUSIONS

The profile diagrams of the four systematically chosen segments of the forest stand show important structural variations within the homogenous vegetation. Three of these structural variations seem to be significant. These can be classified as:

(a) A relatively closed tree fern canopy with scattered mixed species tree groups (e. g. Metrosideros-Cheirodendron and Cheirodendron-Ilex) and lacking an overstory (Fig. 4 and 6).

(b) A closed tree fern canopy with an overstory of emergent koa (Fig. 5).

(c) Closed Metrosideros tree groups with a closed tree fern layer (Fig. 7). This profile probably denotes a "gap-phase" replacement primarily by Metrosideros.

The structural variations described in (a) and (b) were also brought out by Maka (1973) who used a mathematical approach to analyze spatial distribution patterns of woody plant species in the Kilauea rain forest. Pattern (c) was not identified by Maka. This was caused by the properties of Maka's techniques which were related to species ordinations and tests for heterogeneity which are sensitive only to combinations of different species but not to aggregations of individuals of the same species. This shows a limitation of the mathematical approach to identifying spatial distribution patterns. Pattern (c) is an important structural variation indicating "gap-phase" replacement, which is probably an important mechanism in the maintenance of this montane rain forest.

The woody plant distribution by size-classes regardless of species shows a curve sloping from left to right in more or less a straight line (Fig. 12), which if plotted on ordinary graph paper will be approaching the inverse J-shaped distribution characteristic of a stable self-maintaining forest community. Several workers (e.g. Meyer and Stevenson 1943, Meyer 1952, Leak 1964 in North America and Carron 1968 in Australia) have indicated that an inverse J-shaped distribution is characteristic of a well-balanced, self-maintaining forest stand. The stand structure curve for this forest which approaches the inverse J-shaped distribution however, is not necessarily an indication of stability, since it is composed of species with different height- and diameter-growth potentials. That is, a number of the small-sized woody plant species (e.g. Vaccinium calycinum, Broussaisia arguta) will never grow into the tree layers and the low-stature tree species (e.g. Cheirodendron trigynum, Ilex anomala) will never grow into the tall tree layers, because they lack the growth potential. This pattern is generally true for tropical forests, and is reflected in the forest stratification which shows a decreasing number of species with increase in height strata (Richards 1952).

Structural analysis of individual species populations show good stability trends for all low-stature and intermediate-stature tree species, including Metrosideros. Stability trends for low-stature and intermediate-stature tree species are reflected in the inverse J-shaped distributions for these species. Similar population structure trends have been reported for lower story and middle story tree species in rain forests in other parts of the world, for example in Nigeria (Jones 1956). Jones believed that these species were shade tolerant and hence were able to maintain stable populations under the tall canopy in the dark dense forest. The stability trends for low-stature and intermediate-stature tree species in the Kilauea rain forest suggests that these species are also shade tolerant.

Several woody plant species were represented in the population sample with interrupted size-classes. Notably these include three species in the tree fern layer (Cibotium chamissoi, Cyrtandra lysiosepala and Clermontia hawaiiensis) and three species in the low-stature tree layer (Myoporum sandwicense, Myrsine lessertiana and Pelea volcanica). The interrupted size-class distribution for these species merely indicates less overall abundance of these species rather than a lack of self maintenance. A larger area sample may have included all size-classes of individuals of these species. Low overall abundance of species may be brought about by a number of factors including self-thinning mechanisms such as allelopathy (Webb et al. 1967). Thus the low overall abundance of these species may not necessarily indicate that these are seral species in the stand. More autecological information is required in order to assess the successional status of these less abundant species.

The emergent species Acacia koa var. hawaiiensis is not characterized by an inverse J-shaped population distribution curve. But small-sized and intermediate-sized individuals are present. Koa regenerates by seedlings and root suckers in this forest. Both seedlings and root suckers have the potential to grow into tree-sized individuals. Even though a relatively large number of koa seedlings were found in the forest, saplings, and small and intermediate-sized tree individuals were fewer in number. Most of the koa trees were in the emergent layer. This type of size-class distribution has been found to be typical of emergents in tropical forests in the Ivory Coast (Aubréville 1938 cited in Jones 1950, 1956) in British Guiana (Davis and Richards 1933, 1934) and in Nigeria (Richards 1939, Jones 1950, 1956) and in sub-tropical rain forests in Melanesia (Whitmore 1966).

The low numbers of koa saplings and small and intermediate-sized trees can be interpreted as reflecting either

(a) a gradual decline of koa in the forest, or

(b) a rapid growth through the small and intermediate sizes into the emergent layer coupled with high survival of saplings.

The final elucidation of this question can only be determined from permanent plot data. If it is assumed that koa is gradually disappearing in this montane rain forest, it is indeed a very slow process because lower-sized trees are not absent.

Koa seedlings can germinate in the dark and they show rapid height growth under favorable light conditions (Spatz 1973). Diameter increment studies on koa have also shown that a koa tree can reach a diameter of 100 cm Dbh in one hundred years (Spatz and Mueller-Dombois, unpublished data). Their data show that diameter increment is rapid in the first one hundred years, but that it slows down thereafter. About six koa trees per ha in the population reached diameters of 100 cm Dbh and above. These trees were all in the emergent layer. Also, koa trees 40 cm Dbh in diameter reach the emergent layer. This means that the emergent koa trees in this forest stand are definitely not of one generation as is often thought; the emergent koa represent at least two generations. This may account for the fact that Whitesell (1964) found 49% of the saw timber sized koa trees to be rotten. This 49% may represent the older generation koa trees that had attained physiological senility and had subsequently been attacked by insects and fungi.

In addition to points (a) and (b) discussed above, the low number of saplings and small-sized and intermediate-sized koa trees may also reflect "gap-phase" regeneration, as reported for emergents of other tropical forests (Jones 1950, 1956). Webb et al. (1972) have shown experimentally that gap-phase regeneration of emergents is an important phenomenon in subtropical rain forests in Australia. In the Kilauea rain forest, it was observed that a large proportion of the koa saplings and trees had germinated and became established on root collars of scattered, wind-thrown koa emergents. This indicates one type of gap-phase replacement, where there is a 1:1 replacement of koa. This is not the only type of gap-phase replacement possible. Trees could get blown down in groups during heavy storms occurring at longer, but unpredictable intervals. This could create larger gaps where koa regeneration could occur in abundance. The latter type of gap-phase replacement is thought to be an important strategy in maintaining emergent species populations in tropical rain forests (Webb 1958).

In the Kilauea forest, koa seedlings were found on both logs and mineral soil. But survival chances of seedlings on mineral soil seem to be very low, as indicated by the log-soil distribution. This may be due to the rooting activity of the feral pig (Sus scrofa). Pigs destroy koa seedlings mostly by mechanical damage, by trampling or uprooting seedlings. Pigs sometimes also feed on koa root sprouts. The better establishment of koa seedlings on root collars of wind-thrown emergents may also be related to the protection the seedlings receive from pig damage. A similar situation was reported in Australia, where *Nothofagus cunninghamii* trees were better established on root balls of wind-thrown trees than on the forest floor. *Nothofagus* seedlings on root balls are there protected from the scratching activity of lyre-birds (Howard 1973). It could be reasonably assumed that if pig damage is eliminated the survival ratio of koa in the forest would be still more favorable. On the other hand, if pig activity is increased koa will be able to become established only on logs and the species could get rapidly thinned out. This could result in a change of the forest type from an *Acacia-Metrosideros-Cibotium* to a *Metrosideros-Cibotium* type. The change in forest composition caused by pig digging over long periods of time is not unknown. In Europe, cases are known where high pig rooting activity has caused broad-leaved species to be replaced by spruce (Lebedeva 1956 cited in Sukachev and Dylis 1968) and birch to be replaced by oak-beech stands (Vietinghoff-Reisch 1952 in Sukachev and Dylis 1968).

The Kilauea forest is composed almost exclusively of native woody plant species. Few exotic thorn-shrub species such as *Rubus rosaefolius* and *Rubus penetrans* are found in the forest. Of the exotics, *Rubus rosaefolius* is the only species that has a self-maintaining population. But this species is mostly confined to gap areas.

The analysis shows that the *Acacia-Metrosideros-Cibotium* forest could be considered stable at the present time. All native woody plant species show regeneration and maintenance. The majority of species represented as mature, reproducing individuals in the stand are also represented as reproduction (seedlings) and intermediate-sized or -aged individuals. Because of this the forest may be considered a climax i.e. a stage in community development in which the species composition and structure is maintained over a long (unspecified) time in which the species populations are assumed to be in dynamic balance with the prevailing habitat factors and with themselves. There are, however, two major disturbance factors that can be identified in the forest. These are the invasion of exotic plants and the activity of feral pigs. The native plant populations seem to be able to maintain stable populations and check the invasion of exotics into the stand. On the other hand, it can be assumed that due to the long time presence of feral pigs, the forest has changed. Because of this the forest can be better described as disclimax, meaning a climax somewhat offset from its normal expression by a stress factor (feral pigs). At the present time the carrying capacity of the forest is not known. But intensive pig rooting activity over long periods can undoubtably cause a change in the stability relationships, bringing about a deterioration of the native montane rain forest ecosystem.

LITERATURE CITED

Aubréville, A. 1938. La Foret Coloniale: les forets d'Afrique occidentale francaise. Ann. Acad. Sci. Colon., Paris, 9.

Baldwin, P. H. and G. O. Fagerlund. 1943. The effect of cattle grazing on koa reproduction in Hawaii National Park. Ecology 24:118-122.

Berger, A. J. 1972. Birds of the Kilauea Forest Reserve, A progress report. Dept. of Botany, Univ. of Hawaii, US/IBP ISLAND ECOSYSTEMS IRP Tech. Rep. No. 6. 19 p.

Berger, A. J., J. L. Gressitt and D. Mueller-Dombois. 1968. Application to National Science Foundation from B. P. Bishop Museum and the University of Hawaii. International Biological Program, Hawaii Terrestrial Biology Subprogram. Submitted April 18, 1969. 364 p.

Bridges, K. W. and G. V. Carey. 1973. The climates of the IBP sites on Mauna Loa, Hawaii. Dept. of Botany, Univ. of Hawaii, US/IBP ISLAND ECOSYSTEMS IRP Tech. Rep. No. 22, Supp. 1. 141 p.

______________________. 1974. The climates of the IBP sites on Mauna Loa, Hawaii. Dept. of Botany, Univ. of Hawaii, US/IBP ISLAND ECOSYSTEMS IRP Tech. Rep. No. 38. 97 p.

Canfield, R. 1941. Application of the line-interception method in sampling range vegetation. J. For. 39:451-460.

Carron, L. T. 1968. An outline of forest mensuration with special reference to Australia. Australian National University Press, Canberra. 224 p.

Clarke, F. L. 1875. Decadence of Hawaiian Forests. All About Hawaii 1:19-20.

Cline, M. G., A. S. Ayres, V. C. Foster and M. Baldwin. 1955. Soil survey of the territory of Hawaii. U. S. Dept. Agric. with cooperation of Hawaii Agric. Expt. Sta. Soil Survey Series 1939, No. 25. 644 p. + maps.

Cottam, G. and J. T. Curtis. 1956. The use of distance measurements in phytosociological sampling. Ecology 37:451-460.

Davis, T. A. W. and P. W. Richards. 1933. The Vegetation of Moraballi Creek, British Guiana; an ecological study of a limited area of tropical rain forest. Part I. J. Ecol. 21:350-384.

______________________. 1934. The Vegetation of Moraballi Creek, British Guiana; an ecological study of a limited area of tropical rain forest. Part II. J. Ecol. 22:106-155.

Giffin, J. G. 1972. Statewide Pittman-Robertson Program. Hawaii Division of Fish and Game. Project No. W-15-1. 10 p.

Howard, T. M. 1973. Studies in the ecology of _Nothofagus cunninghamii_ Oerst. I. Natural regeneration on Mt. Donna Buang Massif, Victoria. Aust. J. Bot. _21_:67-78.

Jones, E. W. 1950. Some aspects of natural regeneration in Benin rain forest. Emp. For. Rev. _29_:108-125.

__________. 1956. Ecological studies on rain forest of Southern Nigeria. IV. (Con't.) Pt. II. The reproduction and history of the forest. J. Ecol. _44_:83-117.

Knapp, R. 1965. Die Vegetation von Nord-und Mittelamerika und der Hawaii-Inseln. Gustav Fischer Verlag. Stuttgart. 373 p.

Krajina, V. J. 1963. Biogeoclimatic zones of the Hawaiian Islands. Newsletter of the Hawaiian Bot. Soc. _2_(7):93-98.

Lane, I. E. (N. D.) A tentative checklist of ferns and fern-allies of the Hawaiian Islands. Mimeo report. 25 p. (On file with Dr. C. H. Lamoureux, Dept. of Botany, Univ. of Hawaii, Honolulu, Hawaii.)

Leak, W. B. 1964. An expression of diameter distribution for unbalanced, uneven-aged stands and forests. For. Sci. _10_:39-50.

Lebedeva, L. S. 1956. Ecological characteristics of wild boars in Belorezh forest. Uchen. Zap. Mosk. Gorod. Pedag. Inst.

Macdonald, G. A. and A. T. Abbott. 1970. Volcanoes in the sea. The geology of Hawaii. Univ. of Hawaii Press, Honolulu. 441 p.

Maka, J. 1973. A mathematical approach to defining spatially recurring species groups in a montane rain forest on Mauna Loa, Hawaii. Dept. of Botany, Univ. of Hawaii, US/IBP ISLAND ECOSYSTEMS IRP, Tech. Rep. No. 31. 112 p.

Meyer, W. H. 1952. Structure, growth and drain in unbalanced uneven-aged forests. J. For. _50_:85-92.

Meyer, H. A. and W. Stevenson. 1943. The structure and growth of virgin beech-birch-maple-hemlock forests in northern Pennsylvania. J. Agr. Res. _67_:465-484.

Mueller-Dombois, D. 1966. The vegetation map and vegetation profiles _In_ M. S. Doty and D. Mueller-Dombois, Atlas for bioecology studies in Hawaii Volcanoes National Park. Hawaii Botanical Science Paper No. _2_:391-441.

_______________. 1966a. Soils, In M. S. Doty and D. Mueller-Dombois. Atlas for bioecology studies in Hawaii Volcanoes National Park. Hawaii Botanical Science Paper No. 2:93-142.

_______________. 1971. Procedure for sampling the koa-ohia-tree fern forest in Kilauea Forest Reserve, Hawaii (Upper montane rain forest) Part I, Comprehensive plant ecological survey. Dept. of Botany, Univ. of Hawaii, Hawaii Terrestrial Biology Subprogram. US/IBP ORIGIN AND STRUCTURE OF ECOSYSTEMS IRP Tech. Rep. No. 1. 56-77.

Mueller-Dombois, D., R. G. Cooray and J. Crain. 1972. Kilauea rain forest study. Dept. of Botany, Univ. of Hawaii, Island ecosystems stability and evolution subprogram. US/IBP ORIGIN AND STRUCTURE OF ECOSYSTEMS IRP Tech. Rep. No. 2. 50-60.

Mueller-Dombois, D. and V. J. Krajina. 1968. Comparison of east flank vegetation on Mauna Loa and Mauna Kea, Hawaii. Proc. Symp. Recent Adv. Trop. Ecol. Varanasi, India. 508-520.

Nelson, R. E. and P. R. Wheeler. 1963. Forest Resources of Hawaii - 1961. Hawaii Dept. Land and Nat. Res. and U. S. Forest Serv. SW Forest and Range Expt. Sta. Honolulu, Hawaii 48 p. + illus.

Richards, P. W. 1939. Ecological studies on the rain forest of Southern Nigeria. I. The structure and floristic composition of the primary forest. J. Ecol. 27:1-61.

_______________. 1952. The Tropical Rain Forest. Univ. Press, Cambridge. 450 p.

Rock, J. F. 1913. Indigenous trees of the Hawaiian Islands. Published under patronage. Honolulu, T. H. 518 p.

Sato, H. H., W. Ikeda, R. Paeth, R. Smythe and M. Takehiro, Jr. 1973. Soil Survey of the Island of Hawaii, State of Hawaii. USDA Soil Conservation Service in cooperation with Univ. of Hawaii Agric. Expt. Sta. 115 p. + maps.

Scowcroft, P. G. 1971. Acacia koa Gray - Monarch of the Hawaiian Forests - A problem analysis. 21 p. (Mimeo report on file at Office of U. S. Forest Service, PSW, Honolulu, Hawaii.)

Snedecor, G. W. and W. G. Cochran. 1971. Statistical Methods, sixth edition. The Iowa State University Press. Ames, Iowa. 593 p.

Spatz, G. 1973. Some findings on the vegetative and sexual reproduction of koa. Dept. of Botany, Univ. of Hawaii, US/IBP ISLAND ECOSYSTEMS IRP Tech. Rep. No. 17. 45 p.

Spatz, G. and D. Mueller-Dombois. 1973. The influence of feral goats on koa tree reproduction in Hawaii Volcanoes National Park. Ecology 54:870-876.

Stearns, H. T. and G. A. Macdonald. 1946. Geology and ground water resources of the island of Hawaii. Hawaii Division of Hydrography, Bull. 9. 363 p. + map.

St. John, H. 1973. List and Summary of the Flowering Plants in the Hawaiian Islands. Pacific Botanical Garden Memoir No. 1. Pacific Tropical Botanical Garden, Lawai, Kauai, Hawaii. 519 p.

Sukachev, V. N. and N. Dylis. 1968. Fundamentals of forest biogeocenology. (Transl. from Russian by J. M. MacLennan). Oliver and Boyd, Edinburgh and London. 672 p.

Taliaferro, W. J. 1959. Rainfall of the Hawaiian Islands. Hawaii Water Authority. 394 p.

Tomich, P. Q. 1969. Mammals in Hawaii. B. P. Bishop Museum. Special Publication 57. Bishop Mus. Press. Honolulu, Hawaii. 238 p.

____________. 1972. Progress Report: Small Mammals of Kilauea Forest Reserve, October 8, 1971. Dept. of Botany, Univ. of Hawaii, ~~Island Ecosystems Stability and Evolution Subprogram.~~ US/IBP O~~RIGIN AND~~ Island S~~TRUCTURE OF~~ ECOSYSTEMS IRP Tech. Rep. No. 2. 168-170.

Troll, C. 1959. Die tropischen Gebirge. Bonner Geog. Abh., 25.

Vientinghoff-Riesch, A. F. 1957. Untersuchungen über Verbreitung und Schadwirkung des Lärchenblasenfusses (*Taeniopthrips larsivorus* Kart) in den Randzonen seines Verbreitungsgebietes in Norddeutschland, der Schweiz und Frankreich. Z. Angew. Ent. 41. 449-474.

Walter, H. 1971. Ecology of tropical and subtropical vegetation (Transl. from German by D. Mueller-Dombois). Oliver and Boyd, Edinburgh. 539 p.

Webb, L. J. 1958. Cyclones as an ecological factor in tropical lowland rain forest, North Queensland. Aust. J. Bot. 6:220-228.

Webb, L., J. J. G. Tracey and K. P. Haydock. 1967. A factor toxic to seedlings of the same species associated with living roots of the non-gregarious subtropical rain forest tree *Grevellia robusta* J. Appl. Ecol. 4:13-25.

Webb, L. J., J. G. Tracey and W. T. Williams. 1972. Regeneration and pattern in subtropical rain forest. J. Ecol. 60:675-695.

Whitesell, C. D. 1964. Silvicultural characteristics of koa (*Acacia koa* Gray). U. S. Forest Serv., Pacific SW Forest and Range Expt. Sta. Res. Paper PSW-16. Berkeley, Calif. 12 p. + illus.

Whitmore, T. C. 1966. The social status of _Agathis_ in a rain forest in Melanesia. J. Ecol. _54_:285-301.

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APPENDIX 1. -- Pooled Classes and Groupings of 5 cm Dbh Classes under Each Pooled Class for Heterogeneity Chi-Square (ΣX^2) Computations for Tree Species

Species	Pooled class								
	1	2	3	4	5	6	7	8	9
Metrosideros collina subsp. polymorpha	5 cm	10 cm	15 cm	20 cm	25 cm	30 cm	35 cm	40 cm	45-145 cm
Myrsine lessertiana	5-10 cm	15-30 cm	--	--	--	--	--	--	--
Acacia koa var. hawaiiensis snags	5-30 cm	35-60 cm	65-90 cm	95-150 cm	--	--	--	--	--
Acacia koa var. hawaiiensis	5-20 cm	25-40 cm	45-60 cm	65-80 cm	85-100 cm	105-175 cm	--	--	--
Coprosma rhynchocarpa	5 cm	10 cm	15-20 cm	--	--	--	--	--	--
Cheirodendron trigynum	5 cm	10 cm	15 cm	20 cm	25 cm	30-35 cm	--	--	--
Ilex anomala	5 cm	10-60 cm	--	--	--	--	--	--	--
Myoporum sandwicense	5-15 cm	20-50 cm	--	--	--	--	--	--	--

APPENDIX 2. -- Regression Equations

Crown Diameter (m) as a Function of Trunk Diameter (cm) and Substrate of Germination of Six Species* (from Maka 1973)

1.	Metrosideros collina subsp. polymorpha	$y = 1.3 + 0.1x$
2.	Myoporum sandwicense	$y = 2.0 + 0.1x$
3.	Ilex anomala	$y = 0.9 + 0.2x$
4.	Coprosma rhynchocarpa	$y = 2.6 + 0.03x_1 + 0.03x_2$
	x_1 = trunk diameter	
	x_2 = substrate of germination $\begin{cases} \text{soil} = -1 \\ \text{log} = 1 \end{cases}$	
5.	Myrsine lessertiana	$y = 1.0 + 0.2x$
6.	Cheirodendron trigynum	$y = 0.8 + 0.2x$

*The regression equations were derived by the standard procedures for regression from numerous (20-70) measurements of trunk and crown diameters and substrates of each species.

APPENDIX 3

Provisional Checklist of Plants from the 80 hectare IBP Study Site in the Kilauea Forest Reserve, Hawaii, 5,400 feet elevation. Nomenclature of Pteridophytes follows Lane (n. d.) and nomenclature of angiosperms follows St. John (1973). In the first column on left of plant name I-refers to indigenous and X-refers to exotic species. In the second column, T-Trees, S-Shrubs, H-Herbs, C-Woody climber, E-Epiphyte and sP-Semi-parasite.

Algae

Charophyceae
- Nitella sp.

Chlorophyceae
- Spirogyra sp.

Cyanophyceae
- Anacystis dimidiata (Kuetz.) Drouet & Daily
- Palmogloea protruberans (Sm. & Sw.) Kuetzing
- Schizothrix tenerrima (Gomont) Drouet

Fungi

Phycomycetes
- Pilobolus sp.
- Piptocephalis sp.

Lichens

- Cladonia sp.
- Stereocaulon sp.

Bryophytes

Hepaticae
- Anastrophyllum fissum
- Bazzania cordistipula
- Bazzania sp.
- Calypogeia tosana
- Calypogeia sp.
- Dumortiera hirsuta
- Lepidozia australis
- Lophocolea sp.
- Odontoschisma sandvicense
- Pallavicinia sp.
- Symphyogyna sp.

Musci

Campylopus sp.
Hypnum sp.
Leucobryum gracile Sull.
Plagiothecium draytonii (Sull.) Bartr.
Pogonatum sp.
Rhizogonium spiniforme (Hedw.) Bruch.
Thuidium sp.

Anthocerotae

Anthoceros sp.

Pteridophytes

Aspidiaceae

Athyrium microphyllum (Sm.) Alston
Athyrium sandwichianum Presl
Cyclosorus sandwicensis (Brack.) Copel.
Dryopteris glabra (Brack.) Kuntze
Dryopteris paleacea (Sw.) Robinson
Dryopteris sp.
Elaphoglossum hirtum (Sw.) C. Chr. var. micans
Elaphoglossum wawrae (Luerss.) C. Chr. (Mett.) C. Chr.

Aspleniaceae

Asplenium contiguum Kaulf.
Asplenium lobulatum Mett.
Asplenium normalae Don.
Asplenium schizophyllum C. Chr.

Blechnaceae

Sadleria pallida H. & A.

Dicksoniaceae

Cibotium chamissoi Kaulf.
Cibotium glaucum (Smith) H. & A.

Gleicheniaceae

Dicranopteris emarginata (Brack.) Robinson

Grammitidaceae

Adenophorus tamariscianum var. tripinnatifidum (Gaud.) Hlbd.
Grammitis hookeri (Brack.) Copel.
Xiphopteris saffordii (Maxon) Copel.

Hymenophyllaceae

Sphaerocionium obtusum (H. & A.) Copel.
Vandenboschia davallioides (Gaud.) Copel.

Lycopodiaceae

Lycopodium cernuum L.
Lycopodium serratum Thumb.

Marattiaceae
   Marattia douglasii (Presl) Baker

Polypodiaceae
   Pleopeltis thunbergiana Kaulf.
   Polypodium pellucidum Kaulf.

Pteridaceae
   Coniogramme pilosa (Brack.) Hieron.
   Sphenomeris chusana (L.) Copel.
   Pteridium aquilinum var. decompositum (Gaud.) Tryon
   Pteris excelsa Gaud.
   Pteris irregularis Kaulf.

Angiosperms

Apocynaceae

I C Alyxia olivaeformis Gaud.

Aquifoliaceae

I T Ilex anomala H. & A.

Araliaceae

I T Cheirodendron trigynum (Gaud.) Heller

Campanulaceae

I S Clermontia hawaiiensis (Hbd.) Rock
I S Cyanea sp.

Compositae

X H Erechtites valerianaefolia (Wolf) DC.
X H Eupatorium riparium Regel
X H Gnaphalium sp.
X H Hypochoeris radicata L.
I H Senecio sylvaticus L.

Cyperaceae

I H Carex alligata F. Boott
I H Carex macloviana D'Urv.

Epacridaceae

I S Styphelia tameiameiae (Cham.) F. Muell

Ericaceae

I S Vaccinium calycinum Sm.

Gesneriaceae

I S Cyrtandra lysiosepala (Gray) C. B. Clarke

Gramineae

X H Anthoxanthum odoratum L.
X H Axonopus affinis Chase
X H Holcus Lanatus L.

Guttiferae

I H Hypericum mutilum L.

Juncaceae

I H Juncus planifolius R. Br.
I H Juncus tenuis Willd.

Labiatae

I H Phyllostegia floribunda Benth.
I H Stenogyne calaminthoides Gray

Leguminosae

I T Acacia koa var. hawaiiensis Rock
I C Vicia menziesii Spreng.

Liliaceae

I E Astelia menziesiana Sm.

Loranthaceae

I sP Korthalsella complanta (v. Tiegh.) Engler

Myoporaceae

I T Myoporum sandwicense Gray

Myrsinaceae

I T Myrsine lessertiana A. DC.
I S Myrsine sandwicensis A. DC.

Myrtaceae

I T Metrosideros collina subsp. polymorpha (Gaud.) Rock

Onagraceae

X H Epilobium cinereum A. Rich.
X H Ludwigia sp.

Phytolaccaceae

I H Phytolacca sandwicensis Endl.

Piperaceae

I H Peperomia leptostachya H. & A.
I H Peperomia macraeana C. DC.

Polygonaceae

I S Rumex sp.

Rosaceae

I S Rubus hawaiiensis Gray
X S Rubus penetrans Bailey
X S Rubus rosaefolius Sm.

Rubiaceae

I T Coprosma rhynchocarpa Gray
I H Nertera granadensis (L. f.) Druce

Rutaceae

I T Pelea clusiaefolia Gray
I T Pelea volcanica Gray

Saxifragaceae

I S Broussaisia arguta Gaud.

Scrophulariaceae

I H Veronica plebeia R. Br.
I H Veronica serpyllifolia L.

Solanaceae

I T Nothocestrum longifolium Gray
X H Solanum nigrum L.

Umbelliferae

I H Hydrocotyle sibthoripioides [Tourn.] L.

Urticaceae

I S Pipturus hawaiiensis Lévl.

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